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Roman Croitor. A new form of wapiti *Cervus canadensis* Erxleben, 1777 (Cervidae, Mammalia) from the Late Pleistocene of France. *Palaeoworld*, 2020, 29 (4), pp.789-806. 10.1016/j.palwor.2019.12.001 . hal-03126334

HAL Id: hal-03126334

<https://hal.science/hal-03126334>

Submitted on 15 Dec 2022

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A new form of wapiti *Cervus canadensis* Erxleben, 1777 (Cervidae, Mammalia) from the Late Pleistocene of France

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Abstract

A well-preserved antlered braincase of wapiti (*Cervus canadensis*) from the Late Pleistocene of Saint-Hippolyte (Puy de Dôme, France) is described herein. The specific morphology of antlers suggests peculiar adaptations to the open landscapes of periglacial tundra-steppe that permitted to identify a new fossil subspecies *Cervus canadensis combrayicus* n. ssp. The specimen attests the occurrence of *Cervus canadensis* in the paleontological record of Western Europe and helps to clarify the systematical position of some disputed findings of *Cervus* from Western Europe. The revised systematic position of some fossil and sub-fossil cervid findings reveals the paleobiogeographic story of wapiti in Western Europe during the Last Glacial Maximum and the postglacial time. The treeless Alpine altitudes and Sweden are proposed as the glacial refugia for the last European wapiti. The medium-sized deer from Capri Island is regarded as an insular dwarfed wapiti *C. canadensis tyrrhenicus* closely related to the continental form *C. canadensis palmidactyloceros* from the alpine refugium.

Keywords: deer; antlers; Last Glacial Maximum; systematics; megafauna; refugium

1. Introduction

The occurrence of another “elaphine” deer species close to modern *Cervus canadensis* in the paleontological record of Europe was a subject of long-lasting debates since Owen (1846) and then Pomel (1853) reported fossil remains of a large

deer similar to American wapiti. The reports of wapiti from Paleolithic sites of Western Europe were quite frequent over the next decades (Gervais, 1861, 1872; Rivière, 1873, 1905; Belgrand, 1883; De Rance, 1888; Martin, 1893).

Nonetheless, a conservative and more cautious approach to the systematics of the “elaphine” deer (the species complex of *Cervus elaphus* and *Cervus canadensis*) dominated in the zoological literature of the second half of 20th century, where American wapiti and Asian maral and izubr stags were considered as subspecies of common red deer *Cervus elaphus* (Heptner and Zalkin, 1947; Ellerman and Morrison-Scott, 1951; Flerov, 1952; Sokolov, 1959; Geist, 1998). It is still possible to find this type of approach in some recent publications, which regard the subspecies of red deer and wapiti as informal groups “elaphoids” and “wapitoids” (Meiri et al., 2018). The caution apparently was produced by lack of detailed morphological, biological, and ethological studies, while the body size — the only readily available feature distinguishing red deer and wapiti — varies greatly within the better known *C. elaphus* (Heptner and Zalkin, 1947; Flerov, 1952; Geist, 1998). The Middle Pleistocene red deer subspecies *C. elaphus acoronatus* that has similar body size to modern wapiti is a good example of the challenge faced by researchers. Therefore, the exceptionally large remains of *Cervus* from the Late Pleistocene of Europe have often been regarded as an intraspecific variation of red deer (Azzaroli, 1961; Lister, 1987a). Although the presence of two distinct size forms of the “elaphine” deer in the Late Pleistocene of Western Europe has been recognized (Prat and Suire, 1971; Lister, 1987a; Guadelli, 1997), the adequate taxonomical interpretation based on this size difference was not possible due to lack of complete antlers preserving distal portions that provide the main diagnostic characters of “elaphine” deer species and subspecies (Lydekker, 1896; Heptner and Zalkin, 1947; Flerov, 1952; Geist, 1998). Therefore, the question on the occurrence of wapiti in the Late Pleistocene of Europe remained open for more than a century.

The new arguments for the reassessment of systematical criteria for “elaphine” deer were obtained much later when genetic studies revealed an important phylogenetic distance between European red deer and Asian and American wapitis (Kuwayama and Ozawa, 2000; Polziehn and Strobeck, 2002; Ludt et al., 2004; Pitra et al., 2004). The molecular data permitted to reinstate the species status for *Cervus canadensis* (Polziehn and Strobeck, 2002), further supported by biological, ecological and ethological data (Schonewald, 1994; Croitor and Obada, 2018).

Recently, paleogenetic (Stankovic et al., 2011; Meiri et al., 2018) and paleontological (Croitor and Obada, 2018) evidence confirmed the presence of a wapiti closely related to the modern Siberian form of *C. canadensis sibirica/songarica* (the subspecies name spelling *sibirica* and *songarica* is according to the original publication of Severtzoff, 1873, 1876) in the Late Pleistocene of Eastern Europe. Stankovic et al. (2011) regard the arrival of wapiti in Crimea as a part of the invasion of cold-loving forms into Eastern Europe at the end of the Würm II/Würm III Interstadial period.

Nonetheless, despite the numerous old reports of the occurrence of wapiti in the Late Pleistocene of Western Europe, a doubtless demonstration of this “cryptic” mammal dispersal event is still missing (Meiri et al., 2018).

Fossil remains of wapiti from the Late Quaternary of Western Europe were reported under several species and arbitrary names. Owen (1846) described the proximal part of an exceptionally large shed antler with two basal tines (brow and bez) from Kent’s Cavern as a new species *Cervus (Strongyloceros) spelaeus* and suggested close relationships of this specimen with modern wapiti *Cervus canadensis* Erxleben, 1777. Later, Pomel (1853) reported as *Cervus intermedius* de Serres, 1838 some remains of a large deer similar to the American wapiti from several fossiliferous sites of Auvergne (Central France). The species name used by Pomel (1853) is not appropriate. *Cervus intermedius* was mentioned for the first time by de Serres (1838) in the fossil fauna list of the Middle Pleistocene site of the Lunel-Viel Cave and reasonably was regarded by Boule (1892) as a junior synonym of *C. elaphus*. Pomel (1853) provided some diagnostic characters distinguishing the European wapiti from the common red deer: the rugosity of dental enamel, the comparatively larger size of antlers, and the poor development of antler crown as in modern American wapiti. Pomel (1853) indicated several Auvergnian sites where *Cervus intermedius* was found (Tour-de-Boulade, Champeix, caverne de Châtelperron, St-Privat-d’Allier), however, Lunel-Viel was not mentioned among the sites where this species was recorded.

Gervais (1861, 1872) reported a large-sized *Cervus strongyloceros* from the Cave of Pontil near Saint-Pons (Herault, Southern France) and Loubeau Grotto near Mille (Western France), associated with a typical Late Pleistocene fauna. *Cervus canadensis* was reported by Rivière (1873, 1905) from the Paleolithic faunas of Caverne du Cavillon near Menthon and La Muthe Grotto in Dordogne (France). Gaudry (1876) ascribed to *Cervus canadensis* some cervid remains from Louvern : a basal fragment

of very large shed antler with brow and bez tines and an isolated large molar with strong entostyle. The same author (Gaudry, 1880) reported the findings of wapiti from Laugerie-Basse (Dordogne) in association with abundant remains of a horse, as well as with remains of reindeer and saiga. Martin (1893) described a basal fragment of antler of *Cervus canadensis* from the Bassin du Pignon (Hautes-Alpes) and gave some measurements of this specimen: the distance between the brow and bez tines is 23 mm, the maximal diameter of the beam between the bez and brow tines is 55 mm, the minimum diameter of the same part of beam is 40 mm. Belgrand (1883) described a proximal part of antler with pedicle from Genelle in the Seine valley as *Cervus (canadensis) (sic)* noticing the exceptionally large size of the antler (the circumference of the pedicle is 200 mm; the antler beam circumference above the bez tine is 210 mm).

The discussion on the occurrence of the large-sized elaphine deer in France was reopened by Friant (1952, 1957) who regarded the giant cave stag from Kent's Hole as an extremely specialized elaphine deer *Strongyloceros spelaeus* Owen, 1846. Friant (1957) proposed to give Owen's *Strongyloceros* the full genus rank, but this suggestion was not supported (Lister, 1987a).

Prat and Suire (1971) noticed an important and statistically meaningful difference in the dentition and third phalanx sizes recorded in the samples of the elaphine deer collected from different layers of the Paleolithic site Combe-Grenal (Dordogne). Those layers correspond to Würm I and Würm II and have yielded different mammalian faunas that indicate alternating cold and warm climate conditions. The smaller elaphine form that comes from the "Würm I" phase is associated with typically forest fauna, while the large elaphine deer from the "Würm II" stage comes from the deposits characterized by more severe climate conditions. According to Prat and Suire (1971), this size difference may have a taxonomical significance at the subspecies level.

Raynal et al. (1984) confirmed that the Late Pleistocene paleontological record of southwestern France has yielded the remains of two forms of "elaphine" deer distinguished by body size. According to Raynal et al. (1984), the relatively small red deer existed during the phase Wurm I and then was replaced by a larger elaphine deer form ("grand Elaphe") at the beginning of phase Wurm II. The antlered cervid braincase from Saint-Hippolyte belongs, according to Raynal et al. (1984), to the large "elaphine" form associated with "cold" fauna. Raynal et al. (1984) noticed the

poor development of the distal antler crown in the deer from Saint-Hippolyte that differs from the multiaxial crown typical of the modern European red deer, therefore this specimen was arbitrarily described as *C. elaphus acoronatus*. According to Guadelli (1997), the “larger elaphine” deer from Saint-Hippolyte is similar to the large cervid form *C. elaphus* ssp. from Combe-Grenale.

Guadelli (1997) reported some distinctions in dental morphology between “large elaphine” and “small elaphine” forms from Combe-Grenale, such as the relatively linguolabially broader upper molars and very frequent lingual groove in P² in the “large elaphine” deer. Those morphological differences are important since they indicate a stronger brachyodonty (a primitive morphological character) and a more advanced degree of molarization of P² (an advanced morphological character) in the “larger elaphine” deer. Guadelli (1997) also indicated a stronger development of entostyle and a stronger developed lingual cingulum in molars of the “larger elaphine” deer, as well as a paraconid more frequently separated from parastyloid in P₂, a more frequent and higher degree of molarization of P₄ (the metaconid and paraconid are connected and close the second dental valley) that distinguish the “large elaphine” deer from the “smaller” one. Guadelli (1997) estimated the differences in dental morphology as taxonomically significant and proposed the species name *Cervus simplicidens* for the “smaller elaphine” deer from Combe-Grenale.

However, the species name *Cervus simplicidens* is already preoccupied by Lydekker (1876). This is a case of primary homonymy that makes *C. simplicidens* Guadelli, 1997 permanently invalid (ICZN: Article 52.2). Besides that, the selected — or, better to say, available — diagnostic morphological characters Guadelli’s species possesses do not allow to distinguish it from other forms of red deer. The primitive stage of molarization of P₄ indicated by Guadelli (1997) is quite variable in *C. elaphus* and is recorded in varying frequencies in different red deer samples. According to Janis and Lister (1985), the simple unmolarized P₄ is found in 8% of specimens of *C. elaphus* from the Middle Pleistocene of Mosbach (Germany) and in 47% of specimens of red deer from the early Holocene of England. A rather high frequency of unmolarized P₄ is also recorded in the sample of indigenous Early Iron Age Crimean red deer (Croitor, 2016a).

The species status itself of the smaller elaphine deer from Combe-Grenale was a matter of doubts. Armand (1998), who reported the findings of Guadelli’s ‘*C. simplicidens*’ together with larger *Cervus elaphus* from the Mousterian site of

Bourgeois-Delaunay, noticed that the morphology of P₄ in the smaller deer form may be variable and occasionally shows a molarized condition. Steele (2004) noticed that the arguments for the creation of a new species '*C. simplicidens*' are not sufficient, while Monchot (2008) supposed that the small body size of this cervid form may be explained by the clinal body size variation of *C. elaphus*. Becker et al. (2009) regarded '*C. simplicidens*' as a subspecies of *C. elaphus*.

Thus, the question on the taxonomical status and systematical position of the "large elaphine" deer from the Late Pleistocene of France remains unresolved. The present work proposes a new look at the cervid antlered braincase from the Late Pleistocene of Saint-Hippolyte (France) and other puzzling findings of elaphine deer from Europe. Special attention is paid to the morphological peculiarities of antlers of the deer from Saint-Hippolyte that reveal specific ecomorphological adaptations and thus provide arguments that permit the establishment of a new subspecies for the Late Pleistocene wapiti of Western Europe.

2. The site of Saint-Hippolyte

The volcano-sedimentary complex from Saint-Hippolyte is situated at the slope between the Combrailles elevation and the Limagne Plain in the northwestern part of the Massif Central (Puy-de-Dôme, France; Fig. 1) and is of particular interest, since it yields a well-preserved local record of the Würm pleniglacial stage (Raynal, 1988). The site of Saint-Hippolyte represents a sequence of palaeo-lake deposits that formed in a volcano crater erupted at the end of a temperate phase of the Early Würm, 94000 years B.P. The palaeo-lake deposits were accumulated during at least 30000 years (Raynal et al., 1984; Raynal, 1987). The palynological analysis revealed a continuous climate evolution toward cold steppe during all the period of accumulation of palaeo-lake deposits (Raynal et al., 1984; Raynal, 1987, 1988).

According to Raynal et al. (1984), the fauna of Saint-Hippolyte includes Hyaenidae, *Ursus arctos* Linnaeus, 1758, *Rangifer* sp., *Cervus elaphus acoronatus* Beninde, *Bison* sp., *Bos primigenius* Bojanus, *Equus caballus* cf. *germanicus* Nehring, and *Marmota marmota primigenia* Kaup. The remains of horses are dominant in this faunal assemblage.

Deer remains were recovered from the uppermost layers 3 and 2 in association with remains of large bovids and traces of the presence of Mousterian hunters. Raynal (1987, 1988) did not explicitly indicate the stratigraphic provenance of the skull

stored in the Museum of Clermont-Ferrand, however they mentioned that a fragment of female skull of a similar large cervid came from layer 3. The climate conditions at the time of deposit accumulation were cold and dry and corresponded to the Würm Pleniglacial, MIS2 (Raynal et al., 1984; Raynal, 1987).

3. Material and methods

The antlered braincase from Saint-Hippolyte (catalogue number MHLCLFE-R-M118) is stored in the Natural History Museum Henri-Lecoq, Clermont-Ferrand (France). The material herein studied is compared with craniological material stored in the osteological and paleontological collections of the Natural History Museum of London; the National Museum of Natural History, Paris; the Museum of Zoology and Natural History “La Specola” of Florence; the Institute of Zoology, Chişinău, Moldova; and the National Museum of Ethnography and Natural History of Moldova.

The method of cranial measurements is described in detail elsewhere (Croitor, 2018). The measurements of antlers in most cases are taken according to Boeskorov (2005). Some measurements (the circumferences of antler beam above burr, between brow and bez tines, and above bez tine) were taken according to the antler measurement methodology applied by Owen (1846) and Ward (1892). The diagnostic morphological characters of species-level taxa for cervids are selected according to the criteria established by Vislobokova (1990) and Croitor (2006a, 2006b). The crown part of the antler was measured from the base of the first crown to the tip of the last (third) crown tine. Since the third crown tine is destroyed in the specimen from Saint-Hippolyte, the crown part of the antler was measured with approximation from the base of the first crown tine to the tip of the second crown tine.

Abbreviations: br., brow tine; bz., bez tine; CBL, condylobasal length; CFR, circumference; cr., crown tine; D, breadth; DAP, anteroposterior diameter; DLM, lateromedial diameter; dx, right; H, height; itfr, interfrontal suture; L, length; lmbd, lambdoid suture; N, sample size.; sin, left; tr., trez tine.

4. Systematic paleontology

Family Cervidae Goldfuss, 1820

Subfamily Cervinae Goldfuss, 1820

Genus *Cervus* Linnaeus, 1758

Cervus canadensis Erxleben, 1777

Cervus canadensis combrayicus n. ssp.

(Figs. 2, 5A, B, 6, 9F)

1984 *Cervus elaphus acoronatus* Beninde – Raynal et al., p. 105, table 1, figs. 6, 7.

1997 *Cervus elaphus* ssp. – Guadelli, p. 105, fig. 7.

Etymology: The subspecies name *combrayicus* comes from the toponym Combrailles, the low mountain area in the northwest of the Massif Central (Department of Puy-de-Dôme, France) that adjoins the fossiliferous site where the type specimen was discovered.

Holotype: The braincase of a young mature male individual with the almost complete (partially reconstructed) left antler. The distal part of the right antler and the third crown tine of the left antler are missing. The specimen is stored in the Natural History Museum Henri-Lecoq, Clermont-Ferrand (France); catalogue number MHLCLFE-R-M118.

Diagnosis: The body size is large and corresponds to the body size of modern Asian *C. canadensis*. The antlers are more divergent than in other subspecies; the distal part of the beam segment between the bez (second proximal) and the trez (third) tines is almost horizontal. The beam segment between the bez and the trez tines is relatively longer than in other modern and extinct subspecies. The trez (middle) tine is directed sideward, downward and occasionally may be pointed toward the posterior. The trez tine, the first crown tine, and the distal fork are situated in different planes at ca. 45° angles to each other. The crown part of the antler is weak and attains ca. 30% of the antler length. Unlike in modern wapiti, the first crown tine is rather weak and much shorter than the brow and bez tines. The bez tine is the longest and strongest tine of the antler.

Differential diagnosis: *C. c. combrayicus* is distinguished from modern *C. c. sibirica* and *C. c. canadensis* by the relatively more robust antlers, the stronger divergence of beams, the shorter and weaker first crown tine, and the downward direction of the middle tine that may occasionally be pointed toward the posterior. Unlike *C. c. palmidactyloceros*, *C. c. combrayicus* is somewhat larger and lacks the distal palmation. Unlike *C. c. xantopygus*, the new subspecies is characterized by strongly

divergent antler beams and the beam bending between the bez and trez tines and above the first crown tine.

Locus typicus: Saint-Hippolyte (Puy-de-Dôme, Auvergne, France), 460 m of altitude (Raynal, 1988).

Stratum typicum: Late Pleistocene, “final Wurm I”, MIS2 (Raynal, 1987).

Description of the holotype:

The lambdoid and interfrontal sutures are not obliterated yet; the interparietal suture is completely obliterated (Fig. 2). It is not possible to estimate the stage of obliteration of the coronal suture between pedicles because this part of the skull was restored. However, according to Raynal et al. (1984) who studied the specimen before the restoration, this part of the coronal suture was already obliterated. Therefore, the whole stage of the cranial sutures obliteration corresponds to the age of four years in modern red deer (Mystkowska, 1966). Therefore, the specimen under study belongs to a young mature individual.

The frontal bones are concave in the lateral view. The occipital part of the skull is broadened and forms an almost right angle with the skull roof. The shape of the lambdoid suture is trapezoid, a characteristic feature of the genus *Cervus*. The proportions of braincase do not show any important particularities and fit with values of other species of the genus *Cervus* involved in the comparison. However, the braincase behind pedicles in the specimen from Saint-Hippolyte is somewhat broader than in the Asian forms (Fig. 3; Table 1). The frontal bones breadth falls within the variation of the frontal breadth of the fossil wapiti from Siberia and northeast Asia described by Boeskorov (2005) (Fig. 3B).

The pedicles are moderately long (their length exceeds the half of pedicle diameter) that corresponds to the young adult age of the deer. The circumference of pedicles is quite large exceeding the maximal value of the modern sample of Asian wapiti reported by Boeskorov (2005) and approaches the maximal value of the fossil Asian wapiti *C. canadensis* cf. ‘*sibiricus*’ (Fig. 4A). Taking into account the individual age and the robustness of the pedicles of the deer from Saint-Hippolyte, one can assume that its antlers attained the stage of full development but not reached the potential maximum size according to the available data on the ontogenetic development of antlers in modern red deer and wapiti (Sokolov, 1959; Danilkin, 1999; Bender et al., 2003).

The antlers maintain the typical for wapiti bauplan with six tines: two proximal tines (brow and bez tines), a middle tine (trez tine), and three crown tines (Figs. 5, 6). The distal part of the third crown tine is not preserved. The antler measurements are generally similar to measurements of Asian fossil wapiti (Table 2). The total length of the left antler (measured from the antler base to the tip of the second crown tine) amounts to 114 cm. The antler length of the French specimen equals the largest antlers of *C. elaphus maral* measured by Ward (1892), however, it is much more robust than the antlers of modern red deer. The length of the antler from Saint-Hippolyte is rather moderate if compared to the large sample of antlers of modern American wapiti measured by Ward (1892), but the antler beam is generally very robust and corresponds to the stoutest specimens of modern wapiti (Fig. 7A). The length and stoutness of the antlers generally correspond to those of *C. canadensis cherskii* from the Late Pleistocene of northeast Asia and *C. canadensis mongoliae* from the Late Quaternary of China. Nonetheless, the antlers of wapiti from Saint-Hippolyte are less massive if compared to *C. canadensis* ssp. from Climauti II (Moldova) and are much smaller than the type specimen of *Strongyloceros spelaeus* from Kent's Cavern (Fig. 7B).

The antler beams of the specimen from Saint-Hippolyte are remarkably divergent. They are more divergent than antlers of modern *C. canadensis sibirica* and *C. canadensis canadensis*, so their middle portions (below the middle tines) are almost horizontal (Fig. 5). In the area of middle tine, the antler beam turns upward and the distal fork of the antler crown is set almost vertically and oriented in the parasagittal plane. The antler beam becomes remarkably flattened in the areas of the trez tine and the crown tines ramifications as it is seen in wapitis (Croitor and Obada, 2018). The crown part of the beam is significantly compressed from the sides.

The wapiti from Saint-Hippolyte is distinguished from all modern and fossil forms of wapiti involved in the present study by its relatively and absolutely longer distance between the bez and the trez tines (43% of the antler length; Fig. 4B). The crown part attains 30.3% of the antler length. The antler proportions of the wapiti from Saint-Hippolyte are very distinct from those of *C. canadensis mongoliae* (= *C. canadensis fossilis*). Unlike French wapiti, Chinese form is characterized by the relatively short distance between bez and trez tines (21.6% of the antler length), while the distal crown part is very long and attains 55.4% of the antler length. The type specimen of *C. canadensis cherskii* may be regarded as a transitional form between

the French and Chinese wapitis: the beam segment between bez and trez tines attains 32%, while the crown part makes 32% of the antler length (Fig. 8).

The bez-tine is longer than the brow-tine and is situated at a certain distance from it. This character distinguishes the French wapiti from *C. canadensis canadensis*, *C. canadensis mongoliae*, and *C. canadensis cherskii*, which are characterized by the greatest length of the first crown tine. The distance between the brow and the bez tines amounts to 89 mm on the left antler and 83 mm on the right antler.

The trez tine (or the middle tine) in the deer from Saint-Hippolyte is inserted on the dorsal (lower) side of the beam and is pointed sideward and downward. The apical part of the trez-tine of the left antler is turned toward the posterior. This is one of the most peculiar morphological features of *C. canadensis combrayicus*.

The antler crown is uniaxial and is formed by three tines: the longer and stronger first crown tine and a distal fork. The first crown tine is directed sideward, upward and toward the anterior. The distal crown fork is composed of the second and the third crown tines situated in the parasagittal plane. The distance between the first and the second crown ramifications is larger than the length of the second crown tine. The angle between the trez-tine ramification plane and the crown plane amounts to ca. 45°. The angle between the plane of the first crown tine ramification and the plane of the distal fork is approximatively the same.

The antler surface is clearly pearly in their proximal part but becomes smoother in the distal portion of the preserved left antler. The surface of the crown part is not pearly. The longitudinal furrows of blood vessels are well-expressed.

5. Discussion

5.1. Red deer versus wapiti

The biogeographic, genetic, biological and paleontological data suggest that *C. elaphus* and *C. canadensis* represent a typical case of vicarious species. The sharp geographical and genetic division between red deer and wapiti established at least from the pre-LGM times (Meiri et al., 2018). The eastern border of the former species areal and the western border of the latter one moved repeatedly eastwards and westwards with climate changes, therefore the dispersals of *C. canadensis* in Europe could occur several times (Stankovic et al., 2011; Meiri et al., 2018). The vicarious character of distribution in modern faunas and in the paleontological record is mostly

due to the ecological adaptations and ethological distinctions between *C. elaphus* and *C. canadensis* (Geist, 1998). The morphological distinctions between wapiti and red deer are the main challenge. Very little has been done on the comparative morphological study of *C. elaphus* and *C. canadensis*, apparently, because these species were regarded for a long time as subspecies groups within the single species *C. elaphus*. The attention of researchers was focused mostly upon the shape of antlers and linear cranial measurements that were regarded as taxonomic criteria at the subspecies level (Heptner and Zalkin, 1947; Danilkin, 1999). Therefore, the available data on the morphological distinction between those two species are scant and incomplete, while the size distinction may be an insufficient criterion (Fig. 3). Actually, the detailed comparative study of the cranial and dental morphology of wapiti and red deer was never carried out. The report by Guadelli (1997) regarding the differences in molar morphology between “small” and “large” elaphine deer is the only study that brings some data on comparative dental morphology of *C. elaphus* and *C. canadensis*. The relatively linguolabially broader upper molars and the more frequent lingual groove in P² of the “large elaphine” deer observed by Guadelli (1997) are important dental characters since they indicate the stronger brachyodonty (a primitive morphological character according to Vislobokova, 1990) and the more advanced degree of molarization of P² (an advanced morphological character according to Vislobokova, 1990) in the “larger elaphine” deer if compared to European *C. elaphus*. Guadelli’s (1997) observations suggest that the dental morphology characters may be an effective diagnostic tool and require special attention and verification on a larger fossil and modern osteological material.

We know very little about morphological distinctions in cranial morphology between red deer and wapiti. Heptner and Zalkin (1947) reported just some general differences in cranial proportions of modern *C. canadensis* and *C. elaphus*: the skull in wapiti is generally broader and more robust with a somewhat shorter facial part. The ratio of the face length measured from the anterior part of orbit rim to the tips of premaxillary bones (prosthion) to the condylobasal length normally is below 60%, while in red deer this ratio is usually above 60%, especially in the largest red deer subspecies *C. elaphus maral*, although the sample values are overlapping (Heptner and Zalkin, 1947).

The distinctive features in antler morphology are better known. The antlers of *C. canadensis* are distinguished from *C. elaphus* by their generally poor development of

crown that normally consists of three tines arranged in the parasagittal plane (Lydekker, 1896, 1915; Heptner and Zalkin, 1947). The antler crown in wapiti rarely evolves additional tines, more or less compressed from the sides, and often tends to develop palmations in optimal environmental conditions (Heptner and Zalkin, 1947). The type specimen of *C. canadensis merriami* from Arizona, for instance, represents such a variant of the flattened distal portion of antler (Nelson, 1902). According to Geist (1998), the strongest first crown tine in wapitis is a continuation of the antler beam, while the second and third crown tines should be regarded as a bifurcated crown tine situated on the posterior side of the beam. The Geist's viewpoint is confirmed by the paleontological evidence: some of the early ontogenetic stages of antler development in Tibetan wapiti *C. canadensis macneilli* (Geist, 1998, fig. 8.6c) strikingly remind the antler shape of *Cervus magnus* (= *Pseudaxis magnus* Zdansky, 1925) from the late Tertiary of China (Fig. 9A, B). The antlers of *C. magnus* are characterized by the presence of a single basal tine (brow tine), a trez tine, and a small crown tine situated on the posterior side of the distal part of the main beam, which apparently is a homologue of the first crown tine in wapitis of modern type (Fig. 9A). According to Geist (1998) and Di Stefano and Petronio (2002), *C. magnus* is the earliest species of the genus *Cervus*. However, the antlers of *C. magnus* are already too specialized and represent the evolutionary stage of the evolved parasagittal crown as in modern *C. canadensis*. Most probably, *C. magnus* is a direct forerunner of *C. canadensis* and represents the evolutionary stage after the split of red deer and wapiti lineages.

The parasagittal plan of the antler crown in *C. magnus* and *C. canadensis* is different from the transversally oriented distal fork in the primitive subspecies of red deer (*C. elaphus acoronatus*, *C. elaphus bactrianus*) or the multiaxial crown with multiple crown tines in advanced subspecies of *C. elaphus*. The simple transversal distal fork or the evolutionary advanced multiaxial crown represents an important diagnostic character of modern red deer (Lydekker, 1915; Heptner and Zalkin, 1947; Flerov, 1952; Sokolov, 1959; Geist, 1998). However, this morphological feature appeared very early in the evolution of the genus *Cervus*. For example, *Cervus nestii* (Azzaroli, 1947) (= *Cervus abesalomi* Kahlke, 2001) from the Early Pleistocene of Italy and Georgia already developed the transversal *elaphus*-like crown fork but possessed only one basal (brow) tine (Croitor, 2006a). Therefore, the difference in construction and development of crown part in *C. elaphus* and *C. canadensis* indicates

an independent evolutionary development of the antler crown in *Cervus* starting from the three-pointed antler stage that we can see today in *Rusa unicolor* and *Rusa timorensis*. Such an early evolutionary split of the *magnus-canadensis* and *nestii-elaphus* lineages raises a question on how red deer and wapiti acquired the second basal tine: the bez tine, which is a less constant element of antler in both taxa. The most plausible explanation is that there was a genetic exchange between those two lineages, a phenomenon that is often recorded in the animal world (Arnold, 2015). Multiple cases of such interspecific gene exchange within the *Cervus* lineage were recently reported by Hu et al. (2019).

The position of trez tine is a good diagnostic character that distinguishes wapiti from red deer. In *C. canadensis*, the trez tine is inserted on the lateral side of the beam and the plane of trez ramification is clearly situated in a different plane with respect to the parasagittal plane of the crown tines and the brow and bez tines that are set on the anterior side of the beam.

The smooth surface of the distal portion of antler represents another specific morphological feature of wapiti distinguishing it from the completely pearled antlers of the red deer *C. elaphus* (Geist, 1998). Partially pearled antlers are also reported for modern *C. canadensis* from Yakutia, Russia, that evolve surface pearling only in the area of brow and bez tines (Stepanova and Argunov, 2016). The knobby appearance of the red deer antler surface derives from the periosteum of growing antlers that is responsible for the development of the surface pearling or “perlation” (Goss, 1983). The pearled antler surface is a specific morphological feature of *C. elaphus* and some related forms that sometimes are also included in *Cervus*, such as *Rusa unicolor* and *Rusa timorensis*.

5.2. Fossil subspecies of Eurasian wapiti

The past diversity of wapiti is little known. The Late Pleistocene and Early Holocene paleontological record of Eurasia has yielded several forms of *C. canadensis*, however, some of them were misunderstood and here are included in *C. canadensis* for the first time.

5.2.1. *Cervus canadensis mongoliae* Gaudry, 1872 (= *Cervus canadensis fossilis* Zdansky, 1925)

Gaudry (1872) described a series of antler fragments from the late Quaternary deposits of Suen Hoa Fou, northeast China as a new species *Cervus mongoliae*. The best-preserved specimen is a shed antler characterized by the rather straight beam that bears the brow and bez tines, while the trez tine is missing. The specimen is broken at the first crown ramification where antler becomes remarkably flattened as in modern wapiti. The total length of the antler fragment attains 82 cm, while the approximate distance between the bez and crown ramifications (calculated from the figure provided by Gaudry, 1872) attains ca. 75.7 cm. According to Zdansky (1925), *C. mongoliae* is based on an abnormal variant of wapiti antler. Zdansky (1925) reported the frequent occurrence in the Late Quaternary of northeast China of deer remains that show a great affinity with modern *C. canadensis canadensis* and therefore extended the past geographical distribution of Asian wapiti southwards, as far as Henan Province in China. Zdansky (1925) described the fossil Chinese form of wapiti as *C. canadensis fossilis*, however, this subspecies name is preoccupied with *Cervus elaphus fossilis* Goldfuss, 1821 (Goldfuss, 1821). Therefore the name proposed by Zdansky (1925) is invalid. *Cervus canadensis mongoliae* Gaudry, 1872 should be applied to the fossil wapiti from China. The almost complete antler described and figured by Zdansky (1925) is characterized by a rather moderate length, however, its maximum diameter above the burr (74.0 mm) indicates that this specimen is as robust as other Eurasian fossil wapiti antlers (Fig. 7A). The crown part of the antler is well-developed and consists of three large crown tines that lie in the same plane (Fig. 9D). The crown tines are very strong and clearly more robust than the bez and trez tines. The distal crown tine is compressed laterally and terminated with two small prongs. The crown part of the Chinese wapiti attains more than half of the antler length (55%) and represents the main distinctive morphological feature of this subspecies (Fig. 8). The distance between the bez tine and the trez tine in the Zdansky's specimen, however, is remarkably short and the distance between the bez tine and the first crown tine (ca. 485 mm) is significantly shorter than that in the type specimen of *C. mongoliae*. Zdansky (1925) also ascribed to the fossil Chinese wapiti extremely pachyostotic mandibles, but those specimens actually belong to *Sinomegaceros*.

5.2.2. *Cervus canadensis spelaeus* Owen, 1846

Owen (1846) described and figured a basal fragment of an extremely large shed antler from the Late Pleistocene deposits of Kent's Cavern (England) that is

distinguished from the modern European red deer by its extraordinarily large size, approaching to the size of the largest modern North American wapiti specimens. Owen (1846) reported this deer as *Cervus (Strongyloceros) spelaeus*. According to Geist (1998), the cave stag from Kent's Cave was most likely a wapiti. The antler of *C. canadensis spelaeus* bears two basal tines (brow and bez) separated by a certain distance; the circumference of the beam between the brow and the bez tines, according to Owen (1846), measures 381 mm and significantly exceeds the maximal value for modern American wapiti (330.2 mm) reported by Ward (1892) (Fig. 7B). This value exceeds by ca. 30% the circumferences of other fossil forms of wapiti. The circumference above the burr attains 375 mm, thus greatly exceeds the analogous measurements of modern European red deer *Cervus elaphus* Linnaeus, which range between 220 and 230 mm (Friant, 1957). According to Geist (1998), the basal beam circumference indicates a predicted condylobasal length of 528 mm and a body weight of at least 550 kg lean. The circumferences above the burr of other antlers found in Kent's Cavern range from 250 to 300 mm (Lister, 1987a) and correspond to the values of the largest modern American wapitis (Geist, 1998). Besides the exceptionally large size, not much could be said about the cave stag. The distal fragments of wapiti antlers described from the Late Paleolithic site Climauți II are characterized by exceptionally large size and possibly represent a wapiti similar to cave stag. The length of the segment between the bez and the first crown tines amounts to 410 mm and exceeds by ca. 38% the analogous measurement of other known fossil forms of wapiti (Croitor and Obada, 2018). Most of Kent's Cavern fauna from the main cave deposits has a pre-LMG age and is dated back to 50000–25000 years before present (Higham et al., 2011).

Possibly, the mandible 2003-4-420-Sol of a large-sized deer from the Pleistocene of Soleilhac (France) that was originally described as *Megaceros (Megaceroides) solilhacus* by Azzaroli (1979, pl. 3, fig. 2) also belongs to *C. canadensis*. Besides the extremely large size, this specimen from Soleilhac is characterized by a very long diastema. The length ratio between diastema and lower cheek tooth row is 82.6%, approaching the mandible 2003-4-420-Sol to modern red deer and distinguishing it from other Pleistocene large-sized deer (Croitor et al., 2006). The mandible in question comes from the old paleontological collections of Musée Crozatier (Le Puy-el-Velay, Haute-Loire, France), so its exact stratigraphic context is unknown.

5.2.3. *Cervus canadensis cherskii* Boeskorov, 2005

The type specimen of this subspecies comes from the Late Pleistocene of the lower part of Kolyma valley in Yakutia, Russia. According to Boeskorov (2005), this subspecies is distinguished from the modern *C. canadensis sibirica* Severtsov, 1873 (= *C. canadensis canadensis* according to Flerov, 1952) by its larger size, more robust antlers and by the longer distance between the bez and trez tines (Fig. 9E). The antlers of *C. canadensis cherskii* correspond to the most robust specimens of modern American wapiti measured by Ward (1892), however, the antler length falls within the mean values of Canadian wapiti (Fig. 7). The crown part is relatively shorter than in *C. canadensis mongoliae* and attains 36% of the antler length (Fig. 8). The distal part of the third crown tine in the type specimen is terminated by a small fork as in *C. canadensis mongoliae*. The first crown tine is the strongest one as in modern *C. canadensis canadensis*. The bez tine may be almost of the same length as the brow tine or shorter. The trez tine is well-developed and clearly longer than the brow and bez tines. The area of distribution of this wapiti in northwestern Asia ranged from the Lena River to Western Chukotka. The age of findings of *C. canadensis cherskii* corresponds to the Kargin Interglacial stage (55–25 ky BC) (Boeskorov, 2005) characterized by the maximal distribution of forests and bogs in northeastern Asia (Ukrainitseva, 1979).

5.2.4. *Cervus canadensis palmidactyloceros* De Stefano, 1911

Numerous remains of a peculiar deer come from the Late Pleistocene and Early Holocene of Northern Italy and the peat bogs of Switzerland (Rütimeyer, 1861; De Stefano, 1911). The rather heavy antler beams are directed sideward and terminated with a strongly flattened crown segment that bears four tines (Figs. 9C, 10B). This strong divergence of antlers may be seen also in the antlered skull from Settecannelle, Italy (Abbazzi, 1995, figs. 5, 7). De Stefano (1911) reported the remarkably large size of skeletal remains of this deer and the development of a distal palmation that varies in breadth from 142 to 190 mm. All palmations figured by De Stefano (1911) and Abbazzi (1995) generally show a constant shape pattern: three crown tines that terminate palmation are situated in the same parasagittal plane; the first crown tine is the strongest one and in all cases is bifurcated. Sometimes this bifurcation is set in the transversal plane or looks like a small accessory prong of the stronger first crown tine (De Stefano, 1911). The antler tines are comparatively short and the bez tine is often

missing (De Stefano, 1911; Abbazzi, 1995). The condylobasal length and the upper tooth row length of the skull from Settecannelle (Central Italy) figured by Abbazzi (1995; CBL measured from the figure is ca. 430 mm) correspond to the largest individuals of modern *C. canadensis sibirica* (according to the data of Heptner and Zalkin, 1947). The facial part of the skull from Settecannelle is relatively short (59.5% of the CBL length) as in modern wapiti. Some remains of this endemic wapiti form are reported from the Holocene of southern Italy, however, the osteological remains ascribed to *C. canadensis palmidactyloceros* require a thorough revision since the second coeval elaphine deer *C. elaphus maral* Ogilby, 1840 (probably is a senior synonym of *C. elaphus aretinus* Azzaroli, 1961) from Italy developed rather robust crown tines that sometimes look like small palmations (De Stefano, 1911). This morphological parallelism was interpreted by Abbazzi (1995) and Di Stefano et al. (2015) as an intraspecific variation of *C. elaphus*. However, there are some important morphological distinctions between *C. elaphus marallaretinus* and *C. canadensis palmidactyloceros*: the crown part in the Italian maral is multiaxial and richly branched, while in the Alpine wapiti the crown part always consists of three main crown tines aligned in the parasagittal plane. The strongest first crown tine normally is bifurcated and this feature is rather constant in *C. canadensis palmidactyloceros* from Switzerland and Italy. The almost complete (splanchnocranium is missing) subfossil articulated skeleton of an adult male from Balkakra, Scania (Sweden) (Ahlen, 1965, fig. 9) shows a great affinity with Alpine wapiti. The antlers of Swedish wapiti are characterized by a pronounced compression from the sides above the trez tine and the typical for wapiti parasagittal orientation of the crown plane (Fig. 10A). The trez tine is the strongest and the longest one. Unlike the typical form of *C. canadensis palmidactyloceros*, the wapiti individual from Sweden lacks the bifurcation of the first crown tine.

5.2.5. *Cervus canadensis tyrrhenicus* Azzaroli, 1961

Azzaroli (1961) described this dwarfed insular deer from the cave deposits of Capri (Italy) as *C. elaphus tyrrhenicus*. The body size is close to that of *C. elaphus corsicanus* and *C. elaphus barbarus*, however, the teeth are relatively larger (the lower tooth series exceeds in length the largest specimens of modern *C. elaphus* from France), suggesting a rapid and significant body size reduction. Unlike *C. elaphus corsicanus*, the metacarpal bone in *C. canadensis tyrrhenicus* is significantly shorter

than the radius. The third lobe of M_3 is often reduced; P_4 is molarized; the lower premolar series is relatively short and attains 58% of the molar series length; the protocone in upper molars is supplemented with an additional enamel fold (Azzaroli, 1961, table 7, fig. 1) that was never recorded in *C. elaphus*. The antlers are less divergent and characterized by the presence of short brow and trez tines (Fig. 10C). The bez tine is always missing, while the distal part of the antler is extended into a small palmation terminated with three tines situated in the parasagittal plane: the stronger anterior crown tine that represents a continuation of the antler beam, and two smaller tines that have a posterior position on the main antler axis. The parasagittal orientation of crown tines in the dwarfed deer from Capri is remarkable and apparently was noticed by Azzaroli (1961) who dedicated a part of his discussion to morphological features of wapiti. Nonetheless, according to the state of knowledge at that time, the occurrence of a dwarfed wapiti on a Mediterranean island was incredible, so Azzaroli (1961) assumed that the dwarfed deer from Capri was phylogenetically related to *C. elaphus aretinus* from the Late Pleistocene of Italy. However, *C. elaphus aretinus* is characterized by a multiaxial crown and may be very close to, or even synonymous with, *C. elaphus maral* (Croitor and Cojocaru, 2016). The fossil and subfossil remains of *C. elaphus maral* from Italy were reported by De Stefano (1911), therefore, the synonymy of *C. elaphus aretinus* and *C. elaphus maral* should not be excluded. The shape of the flattened distal portion of antlers of *C. canadensis tyrrhenicus* shows a clear affinity with antler morphology of *C. canadensis palmidactyloceros*: the strong anterior crown tine corresponds to the strongest first crown tine in continental wapiti that represents a continuation of the antler beam; the second smaller crown tine is actually a homologue of the accessory prong or bifurcation of the first crown tine in *C. canadensis palmidactyloceros* (Fig. 10B). The lowermost posterior crown tine in *C. canadensis tyrrhenicus* is a simplified homologue of the distalmost part of antler in continental wapiti (second and third crown tines). This part of antler in *C. canadensis tyrrhenicus* is reduced in size and has lost the bifurcation usually reported as the second and the third crown tines in continental wapitis. The isolation of the island population of Italian wapiti, apparently, occurred during the post-Glacial sea level rise.

5.2.6. *Cervus canadensis combrayicus* n. ssp.

This extinct form of wapiti is generally as large as *C. canadensis cherskii* and modern *C. canadensis sibiricus* and by 11–15% larger than *C. canadensis palmidactyloceros* (Fig. 3). The estimated body mass of *C. canadensis combrayicus* based on the occipital height is ca. 364 kg according to the methodology proposed by Janis (1990). The comparatively smaller antlers of the French wapiti may reflect the rather young individual age of the type specimen (Fig. 7A). Unlike *C. canadensis mongoliae*, the wapiti from Saint-Hippolyte is characterized by relatively shorter crown part and the relatively and absolutely longer proximal portion of the antler between the bez and the trez tines. *C. canadensis cherskii* has rather an intermediate position between the extreme forms of antler shape seen in *C. canadensis mongoliae* from one hand, and in *C. canadensis combrayicus* from another hand (Fig. 8). Unlike both *C. canadensis mongoliae* and *C. canadensis cherskii*, the French wapiti is distinguished by the relatively small size of the first crown tine that is deviated sideward and therefore is not situated in the same parasagittal plane with other two crown tines (Fig. 9F). The trez tine in *C. canadensis combrayicus* is much smaller and is directed downward and represents a peculiar feature of this fossil form.

Unlike modern *C. canadensis canadensis* and closely related *C. canadensis sibirica*, the French fossil wapiti is characterized by a much stronger divergence of antlers, the longer distance between the bez and trez tines, the downward direction of the trez tine, which is comparatively much shorter, and the weak development of the first crown tine, which is pointed more sideward and therefore deviates from the plane of other two crown tines. The difference from modern *C. canadensis xantopygus* is much deeper: besides the all above-mentioned distinctions from other modern wapitis, *C. canadensis combrayicus* is distinguished from *C. canadensis xantopygus* by curved antler beams between the bez and trez and above the trez tine. Certain parallelism may be seen in the weak development of the crown part of antler in both *C. canadensis combrayicus* and *C. canadensis xantopygus*. The strongly divergent antlers of the French wapiti remind the *C. canadensis palmidactyloceros*, however, the deer from Saint-Hippolyte is distinguished from the Alpine wapiti by the lack of distal palmation, the downward direction of the trez tine, and the unbranched first crown tine.

5.3. Functional morphology of antlers and paleoecology of the wapiti from Saint-Hippolyte

The morphological peculiarities of antlers of *C. canadensis combrayicus* represent interesting evolutionary specializations that require a special discussion. The main paleoecologically meaningful antler specializations are the strong divergence of antlers, the relatively long distance between the bez and the trez tines, the short trez tine directed downward, and the sideward deviation of the first crown tine. Here I propose a discussion of the functional significance of morphological specializations of the antlers of the wapiti from Saint-Hippolyte.

The antler spread in the stag from Saint-Hippolyte attained about 205 cm, while the antler spread in modern American wapitis hardly exceeds 130 cm (Ward, 1892). According to Lister (1987b), outstretched antlers are indicative of adaptation of cervids to open landscape, since in forest they would impede movement. Therefore, *C. canadensis combrayicus* shows a more pronounced adaptation to open landscapes than modern wapitis. The specific shape of antler tines in the wapiti from Saint-Hippolyte, however, cannot be explained directly by the adaptation to open landscape and requires a broader discussion of their functional significance in Cervidae and in the deer from Saint-Hippolyte in particular.

According to Davitashvili (1961), the branched and complicated antlers in the advanced cervids represent a specific adaptation that “softens” the sexual selection and diminish the excessive male mortality during the intraspecific combats. The most proximal antler tine (brow tine) appears very early in the cervid evolution and has a function of the locally very restricted protection of eyes and face during combats (Lister, 1987b). The second proximal tine, the bez tine, is specific only for *C. elaphus* and *C. canadensis* and appears in the evolution of *Cervus* during the early Middle Pleistocene simultaneously with a significant body size increase. The estimated body mass of primitive small-sized *Cervus nestii* was about 60 kg (Croitor, 2018), while the body mass of the most ancient subspecies of red deer *C. elaphus acoronatus* attained ca. 237 kg (the body mass is estimated on the basis of occipital height; the sample includes the cranial material from the Tiraspolian gravel and specimens studied by Di Stefano and Petronio, 1992; N total =14). Therefore, a ca. four-time body size increase is observed in the *C. nestii*–*C. elaphus* lineage during the Early Pleistocene–early Middle Pleistocene transition. Petrie (1988) assumed that the costs of intraspecific contests may be relatively greater for larger animals that may have a greater capacity to injure each other. This, probably, may explain why red deer (and, apparently, wapiti too) acquired the second basal tine enhancing the face protection

during combats. It is interesting to notice that the bez tine has a trend to be diminished in European red deer during Late Pleistocene and Holocene simultaneously with body size reduction (Lister, 1987b). Nonetheless, the direct relationship between the body size and the strength of the bez tine in red deer cannot be considered as proved, since the bez tine is quite weak in the largest modern red deer subspecies, *C. elaphus maral* (Heptner and Zalkin, 1947; Flerov, 1952). Lister assumed that the reduction of bez tine in red deer is correlated with the development of richly branched antler crown, but, again, the example of *C. elaphus maral* does not support this hypothesis. Nonetheless, the bez tine in *C. canadensis combrayicus* is particularly strong and long, a feature that distinguished the stag from Saint-Hippolyte from Late Pleistocene European red deer.

In turn, the trez (or middle) tine appears in the evolution of the subfamily Cervinae quite early as an additional second ramification and coincides with the increase of body size and the reduction of upper canines when male antlers became the only dangerous weapon against conspecific rivals (Geist, 1971). Apparently, the development of this tine in the early stages of cervid evolution also must increase the safety of both combatting stags that attained a certain body mass threshold that increases the risk of lethal wounding. The protection function of the trez tine against the rival's antlers was suggested by Kitchener (1987) also for the cervids that bear highly evolved complicated antlers, such as red deer and giant deer. Davitashvili (1961) demonstrated the importance of the additional antler tines in red deer stags by the examples of old bucks with degenerated and simplified antlers that can easily wound and kill their conspecific rivals. A forwardly pointed tine situated in the middle of the antler beam appeared several times independently in the evolution of cervines. This is the case of the middle tine of *Praemegaceros verticornis* from the Middle Pleistocene of Europe, that appeared quite late in the *Praemegaceros* lineage, as it is completely absent in *P. pliotarandoides* from the late Early Pleistocene (Croitor, 2006b). The middle tine of *P. verticornis* is analogous to the trez tine of *C. elaphus* and *C. canadensis* and, apparently, it had the same function of locking of rival's antlers, but is not homologous, since its evolutionary story is different. The evolutionary importance of the middle tine may be confirmed by the fact that many insular dwarfed deer with diminished and simplified antlers maintain the middle tine, which may be the only remained additional branch in the extreme cases of antler simplification (Azzaroli, 1961; van der Geer, 2018).

It is important to note, that the trez tine or its analogues normally evolved in cervids from the middle latitudes and is not present in southern lineages with large antlers, such as *Rucervus* and *Panolia*. A possible explanation is that the male survival is exposed to a stronger pressure in cervids from the temperate latitudes with cold winters and a seasonal drop of forage. The pressure of seasonal male mortality (especially of young and prim-adult age) is important (Clutton-Brock et al., 1982), so the additional security adaptations in antler shape diminish the excessive loss of males during the combats and therefore compensate the seasonal male mortality. Therefore, one can assume the direct relationship between the harder environmental conditions with a seasonal drop of temperatures and forage availability and richly branched antlers. The consequences of seasonality in the southern latitudes are less costly for deer stags, and apparently, this may explain the smaller number of ramifications and the absence of the “second-level protection” tine (the trez tine or its analogues) in large South Asian deer species.

Concerning the wapiti from Saint-Hippolyte, there are doubts if its short and downward-directed trez tine was an effective protection against antlers of stag rivals: in the combat posture of antlers, the trez tines in *C. canadensis combrayicus* are directed backwards. Such a specific position of the trez tine may be explained by its newly acquired function. Apparently, the majority of deer adapted to more or less open landscapes evolve the so-called posterior tine situated on the back side of the beam and positioned below the crown part of the antler (Croitor, 2018). Usually, antlers are more or less sharply bent in the area of the posterior tine, which is situated on the convex side of the antler bow. The posterior tine appears independently in several cervid lineages of the both Cervinae and Capreolinae subfamilies (genera *Rangifer*, *Megaloceros*, *Praemegaceros*, *Praedama*, *Sinomegaceros*, some species of the genus *Dama*). In some cases, the lowermost posterior crown tine may have a position similar to that of the posterior tine seen in the Pleistocene fallow deer: this tine in *Dama geiselana* and *Dama clactoniana* is normally very large, strong and detached from the palmation (Leonardi and Petronio, 1976; Pfeiffer, 1998). The occurrence of a posterior tine and its analogues apparently does not depend on body size (it is developed in the giant continental *Praemegaceros* and *Megaloceros*, in some small-sized insular dwarfs, and in medium-sized *Rangifer*) and is not correlated with the development of palmations or other parts of antlers. The stability of development of posterior tine within the individual variation range (for instance, in

the series of antlers of *Megaloceros giganteus* figured by Reynolds, 1929) suggests an important evolutionary selection in favour of this character, which appeared repeatedly and independently in several lineages of the family Cervidae. Therefore, one can assume a certain biological importance of this part of antlers. The adaptation to more or less open environments is the only circumstance that unites the deer with posterior antler tine. The most plausible explanation of the iterative development of the posterior tine during the evolution of cervids is its specific function of the defense against ectoparasites in rutting males. The study of rutting males of North American deer and territorial African antelopes revealed that the involvement of males in rutting decreases the behavioural and immune defense of males against ticks, which distract them from the rutting behaviour and bring damages to their physical and health state (Hart, 1997; Mooring et al., 2004). The priority of the investment into the rutting activity over the antiparasite defense has a negative consequence for males, which are exposed to a greater parasite load. Rutting impala males, for example, which self-oral groomed at one-third the rate of females, were found to carry about six times more adult ticks than females (Hart, 1997). Observations on male white-tailed deer reveal they had about 3 times as many adult ticks as females (Main et al., 1981). Mooring et al. (2004) suppose that the elevated testosterone level in rutting stags suppresses the grooming behaviour in order to increase male's vigilance, so the increased ectoparasite burden is a frequent side effect in rutting males. It is interesting to notice that the scratch grooming in males of the observed species was not affected by the rutting behaviour (Hart, 1997). One can assume that the posterior tine in cervids is a specialized adaptation for scratch grooming in rutting males that eventually indirectly increase their combat capacities (Croitor, 2016b). Apparently, the evolutionary acquisition of the scratch grooming tine (the posterior tine) indirectly influenced mating success by diminishing of the ectoparasite burden and improving the vigilance and physical state of the rutting stags. According to the available bibliographic data, the disturbing effect of ectoparasites during the rutting period may be important. The observations upon modern North American wapiti revealed that September and October constitute the peak time for feeding by larvae of winter tick *Dermacentor albipictus* (Mooring and Samuel, 1998). This stage of the parasite biological cycle coincides with the rutting season in elaphine deer (Flerov, 1952; Sokolov, 1959) and therefore has an important negative influence over the physical state and the rutting success of stags. The use of antlers for scratch grooming is rarely reported for modern

cervids, which are mostly adapted to wooded and ecotone habitats (Mooring et al., 2004), but it is recorded in *Rangifer tarandus tarandus*, the only modern deer adapted to open environments (Kynkäänniemi et al., 2014). The downward-directed trez tine in *C. canadensis combrayicus*, apparently, got the function of removal of flying parasites and ticks analogous to that of the posterior tine in other Pleistocene giants and in modern reindeer.

The reduced size of first crown tine in *C. canadensis combrayicus* is an advanced evolutionary specialization. The first crown is deflected sideward and a little toward the anterior and spatially is detached from the second and third tines that are directed toward the posterior. A most plausible explanation of the modifications in the crown part of the antler is the acquired clutch function by the first crown tine that becomes in *C. canadensis combrayicus* a functional analogue of the trez tine in other subspecies of wapiti and in red deer. Therefore, the wapiti from Saint-Hippolyte shows the most advanced adaptations to the open landscape within the genus *Cervus* and the evolutionary specialization of its antlers involved the changes in shape and function of the trez and the first crown tine.

5.4. Paleobiogeography and evolution of wapiti in Eurasia

The paleogenetic studies revealed a close relationship of the modern Asian wapiti with the Late Pleistocene *C. canadensis cherskii* and the pre-Last Glacial Maximum specimens from Romania and Crimea (Stankovic et al., 2011; Meiri et al., 2018). The area of distribution of Asian wapiti *Cervus canadensis sibirica* Severtzoff, 1873 (including the darker coloured *C. canadensis songarica* Severtzoff, 1873) today is limited to the mountains that range from Tian-Shan and Altai to Sayan and southern Transbaikal Area (Heptner and Zalkin, 1947; Flerov, 1952; Danilkin, 1999). Therefore, the area of distribution of the lineage of Asian wapitis during the Glaciation epoch was extremely vast and ranged from Chukotka in Northeast Asia to Western Europe (Fig. 11). From the biogeographic point of view, it means that the modern Siberian wapiti should be regarded as a remnant of the successful Ice Age megafaunal species, which survived the Holocene climate warming in the mountains of Central Asia that act as a glacial refugium. 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. This assumption was confirmed by Pavelková Řičánková et al. (2014) who reported a

marked similarity in ecological structure between Recent eastern Altai-Sayan mammalian assemblages and Pleistocene faunas. The Last Glacial and recent eastern Altai-Sayan faunal assemblages are peculiar in the co-occurrence of large herbivore and predator species associated with steppe, desert and alpine biomes. According to Pavelková Řičánková et al. (2014), the relic glacial fauna seems to persist up to present in the Eastern part of the Altai-Sayan region where, for instance, reindeer and saiga antelope still live in sympatry.

The occurrence of the cold-adapted *Cervus canadensis* in Europe during the Last Glacial Maximum explains the “paradoxical” record of elaphine deer in the southern extension of permafrost areas in Eastern Europe, namely in the Late Paleolithic sites Rașcov 7 and Cosouți from Moldova (Sommer and Nadachowski, 2006; Sommer et al., 2008). Banks et al. (2008) elaborated the ecological niche modelling of red deer during the Last Glacial Maximum that does not support the hypothesis of the “East Carpathian Last Glacial Maximum refugium” of *Cervus elaphus*. The elaphine remains from the Late Paleolithic sites of Moldova are very scanty and represented by a few poor and isolated teeth and bone fragments (David, 1980). The recently described antler fragments of *C. canadensis* from the Moldavian Late Paleolithic site of Climăuți (Croitor and Obada, 2018) urges a reconsideration of the elaphine remains from the Late Glacial Maximum of the East Carpathian area.

Wapitis became extinct postglacially in the vast North Eurasian area as Late Pleistocene horses and steppe bison did. However, the relatively abundant subfossil remains of *C. canadensis palmidactyloceros* from Switzerland and Italy, as well as the articulated skeleton with antlers from southern Sweden indicate that the Alpine altitudes and Scandinavia, apparently, served as postglacial refugia for wapiti in Western Europe. The retraction of European wapiti after the post-Pleistocene climate warming into the cool treeless alpine altitudes and its ecological and biological isolation from European red deer may explain the puzzling results obtained by Drucker et al. (2011). The multi-isotope analysis of bone collagen revealed a meaningful difference in paleoecology and paleoenvironment of the postglacial elaphine deer samples from Jura and western Alps (Drucker et al., 2011). According to the obtained results, *C. elaphus* from French Jura inhabited the dense forests in warmer and ecologically more productive ecosystems, while the “red deer” from the Alps persisted in the open landscape and rather cool conditions with low soil productivity by dwelling at higher altitudes than before the climate warming. Drucker

et al. (2011) explained this difference in response to the postglacial climate change as remarkable ecological flexibility of red deer and, possibly, as a specific selection by prehistoric human hunters who preferred to hunt red deer in open areas for technical and/or cultural reasons. Most probably, the postglacial elaphine remains from the high Alpine altitudes belong to the remnant population of *Cervus canadensis* that survived during the early stages of Holocene in the Alpine refugium. Therefore, *C. canadensis palmidactyloceros* from Switzerland, Italy, and possibly French Alps, is a relict population of wapiti that survived in Europe to the Holocene climate warming (Fig. 12). Most probably, dense broad-leafed forests were the main limiting factor for *C. canadensis* in Europe.

6. Conclusions

The new look at the fine antlered stag skull from Saint-Hippolyte permits to close the long-lasting debate of occurrence of wapiti *Cervus canadensis* in the paleontological record of Western Europe. The specific features of antler morphology (the very strong divergence of antler beams, the relatively long antler segment between the bez and the trez tine; the relatively short crown tine of antler; the short downward-directed trez tine and the reduced size of the first crown tine) indicate the advanced adaptations of the wapiti from Saint-Hippolyte to open environments of the Late Pleistocene periglacial ecosystems. The revealed specific evolutionary adaptations are taxonomically meaningful and distinguish the deer from Saint-Hippolyte from all fossil and modern subspecies of wapiti, therefore a subspecies name *Cervus canadensis combrayicus* n. ssp. is proposed for this cervid form. The taxonomical status and exact diagnosis of the extremely large *C. canadensis spelaeus* Owen, 1846 from Kent's Cavern, England, is not clear yet due to the incomplete paleontological material.

The confirmed occurrence of wapiti in the Late Pleistocene of Western Europe answers some questions on evolution and paleoecology of the so-called “elaphine” deer, including the different ecological reaction of lowland red deer and highland Alpine populations of *Cervus* to the postglacial climate change and the conflicting hypothesis on the Last Glacial Maximum refugium for red deer in the East Carpathian Area. The specific adaptations of *Cervus canadensis* to the cold periglacial tundra-steppes explain perfectly the above-mentioned discrepancies.

Alpine treeless altitudes acted as the last refugium for wapitis in Europe during the postglacial time. The endemic Alpine wapiti is represented by *C. canadensis palmidactyloceros* De Stefano, 1911 that maintains the strong divergence of antler beams and acquires the small palmation on the distal part of antlers. The subfossil remains of a wapiti with palmed distal portions of antlers from southern Sweden suggest that the Scandinavian Peninsula was another postglacial refugium for remnant populations of wapiti. Apparently, the last European wapitis were the poor ecological competitor with *C. elaphus* in the conditions of expanded forests. It is not clear yet why *C. canadensis palmidactyloceros* dispersed almost over the entire area of the Italian Peninsula. Apparently, the expansion of wapiti from its Alpine glacial refugium was triggered by a brief return to glacial conditions during the Younger Dryas and the poor development of forests in Italy. The postglacial rise of sea level caused the insular isolation of the dwarfed wapiti *C. canadensis tyrrhenicus* Azzaroli, 1961 from Capri Island. The insular wapiti inherited the distal antler palmation and shape from its continental forerunner *C. canadensis palmidactyloceros*.

The modern Asian wapiti *C. canadensis sibirica* is one of few relic elements of Ice Age megafauna that survived until present in the specific condition of the Tian-Shan/Altai/Sayan glacial refugium that still maintains environmental and faunal features characteristic of the Late Pleistocene tundra-steppe biome.

Acknowledgements

I am very thankful to Michael Lebras and Charles Lemarchand (Museum of Natural History Henri-Lecoq, Clermont-Ferrand) for the granted access to the fossil specimen that is under their care and for the kind assistance during my work. I thank Prof. Wei Dong and an anonymous reviewer for their comments and suggestions that improved the manuscript. This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

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Figure captions

Fig. 1. The geographical location of the paleolake and fossiliferous site Saint-Hippolyte.

Fig. 2. The braincase of *Cervus canadensis combrayicus* n. ssp. (holotype, catalogue number MHLCLFE-R-M118). (A) Dorsal view; (B) side view; (C) occipital view.

Fig. 3. The cranial measurements of *Cervus canadensis combrayicus* n. ssp. compared to the modern and fossil forms of wapiti and red deer. (A) Braincase breadth; (B) frontal breadth; (C) occipital breadth. The data on *C. elaphus priscuslaretinus*, *C. canadensis canadensis*, and a part of data on *C. elaphus acoronatus* and *C. elaphus elaphus* are adapted from Di Stefano and Petronio (1992); the data on *C. canadensis sibirica* and *C. canadensis cherskii* are adapted from Boeskorov (2005); the data on *C. canadensis palmidactyloceros* are adapted from Rüttimeyer (1861) and Abbazzi (1995).

Fig. 4. The pedicle and antler size of *Cervus canadensis combrayicus* n. ssp. compared with modern and fossil wapitis. (A) Pedicle circumference in the correlation with the antler circumference above burr; (B) length of bez-trez antler segment in the correlation with the antler circumference above burr. The data on *C. canadensis* cf. *sibirica* and *C. canadensis cherskii* from the Late Pleistocene of Siberia and modern *C. canadensis sibirica* and *C. canadensis canadensis* are adapted from Boeskorov (2005); the data on *C. canadensis* from the Seine Basin (France) are adapted from Belgrand (1883).

Fig. 5. The antlers of *Cervus canadensis combrayicus* n. ssp. (holotype; A, frontal view; B, upper view of the distal part) compared to modern *Cervus canadensis sibirica* (C; adapted from Stepanova and Argunov, 2016).

Fig. 6. The side view of the holotype of *Cervus canadensis combrayicus* n. ssp.

Fig. 7. The antler size in modern and fossil red deer and wapitis. (A) Antler length plotted against the beam circumference measured between the brow and bez tines; (B) the comparison of antler circumference between brow and bez tines including the incomplete antlers. The data on modern *C. elaphus* and *C. canadensis* are adapted from Ward (1892); the circumference of *C. canadensis mongoliae* is estimated from the maximum diameter of antler above the burr reported by Zdansky (1925). The measurements of *C. canadensis merriami* from Arizona are adapted from Nelson (1902). The circumference of *C. canadensis spelaeus* is adapted from Owen (1846).

Fig. 8. The antler segments of *Cervus canadensis combrayicus* compared to *C. canadensis cherskii* and *C. canadensis mongoliae*.

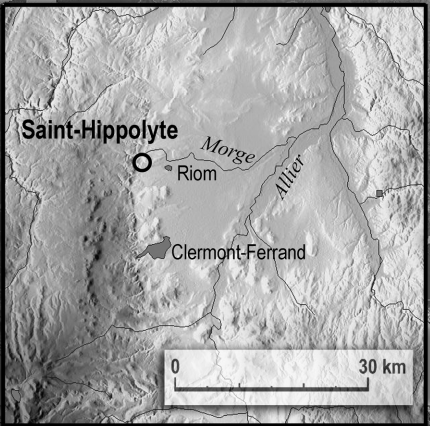
Fig. 9. The antler bauplan and specific morphological peculiarities of fossil Eurasian wapiti and wapiti-like deer. (A) *Cervus magnus* (adapted from Zdansky, 1925; inverted image). (B) Antler of an extant MacNeill's stag *Cervus canadensis macneilli* (adapted from Geist, 1998; inverted image). (C) *Cervus canadensis palmidactyloceros* (adapted from De Stefano, 1911). (D) *Cervus canadensis mongoliae* (adapted from

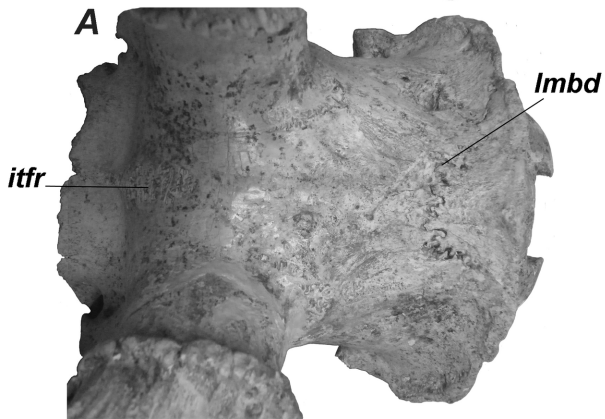
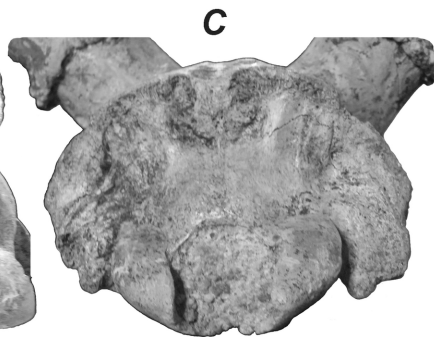
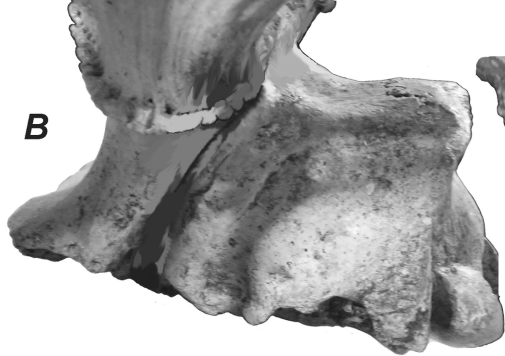
Zdansky, 1925). (E) *Cervus canadensis cherskii* (adapted from Boeskorov, 2005). (F) *Cervus canadensis combrayicus* n. ssp., the median side of left antler (holotype).

Fig. 10. The Holocene forms of wapiti from Western Europe. (A) Antler of subfossil wapiti from Balkakra, Sweden (redrawn from Ahlen, 1965). (B) Reconstruction of antler of *Cervus canadensis palmidactyloceros* based on specimens figured by De Stefano (1911). (C) Antlered frontlet of dwarfed *Cervus canadensis tyrrhenicus* from the Island of Capri (adapted from Azzaroli, 1961).

Fig. 11. The maximum area of distribution of wapiti in Eurasia and the actual area of distribution of *Cervus canadensis sibirica* in the Tian-Shan/Altai/Sayan postglacial refugium.

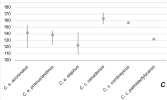
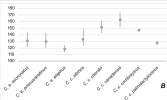
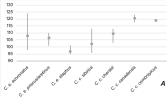
Fig. 12. Chronological distribution of *Cervus canadensis* in different parts of Europe. The extensive dashed line indicates the unprecise dating of fossil remains from Kent's Cavern (Higham et al., 2011). The time span of wapiti presence in Sweden is hypothetical.

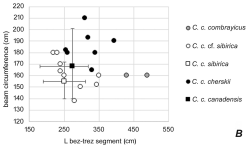
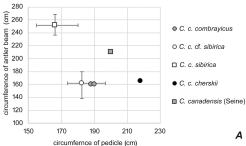


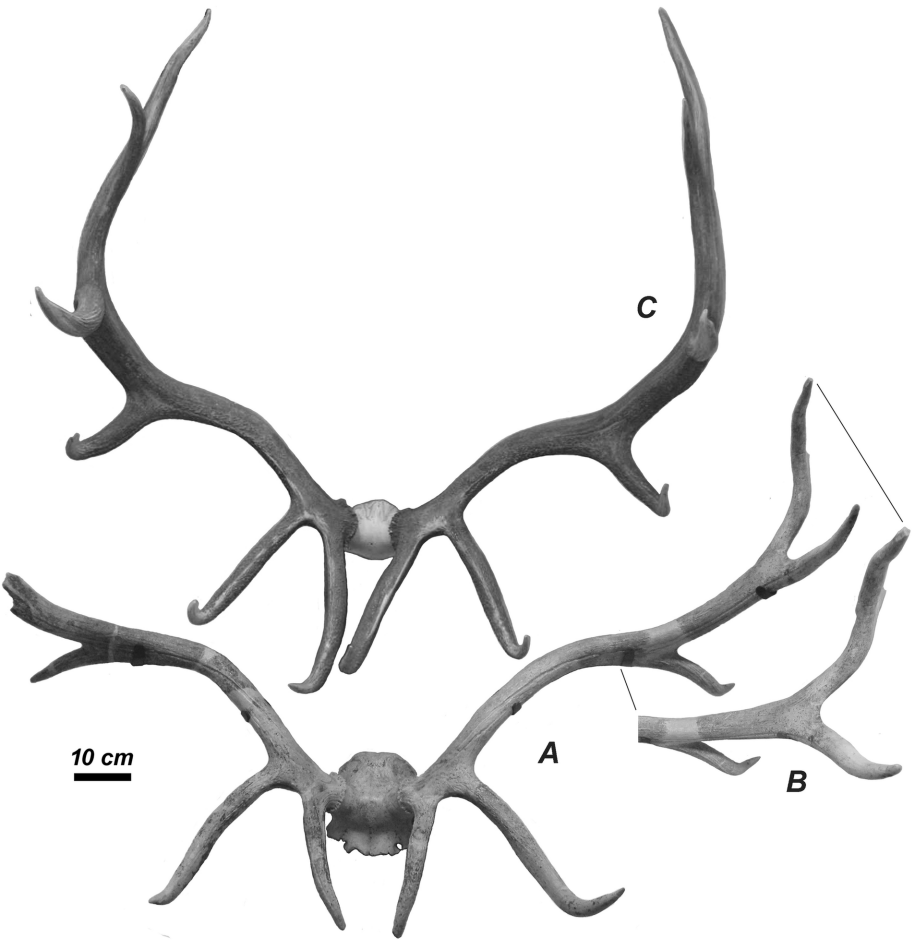


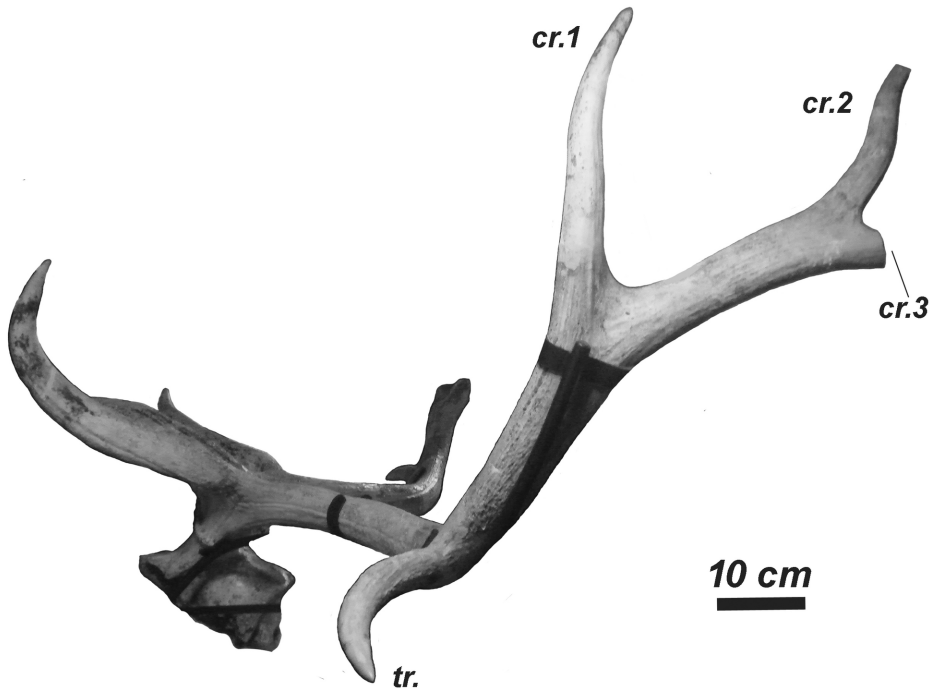
10 cm

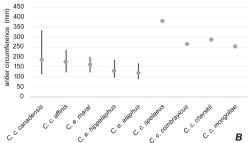
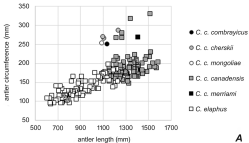
A thick black horizontal line representing a scale bar, positioned below the text '10 cm'.

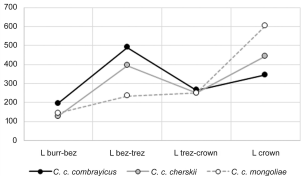


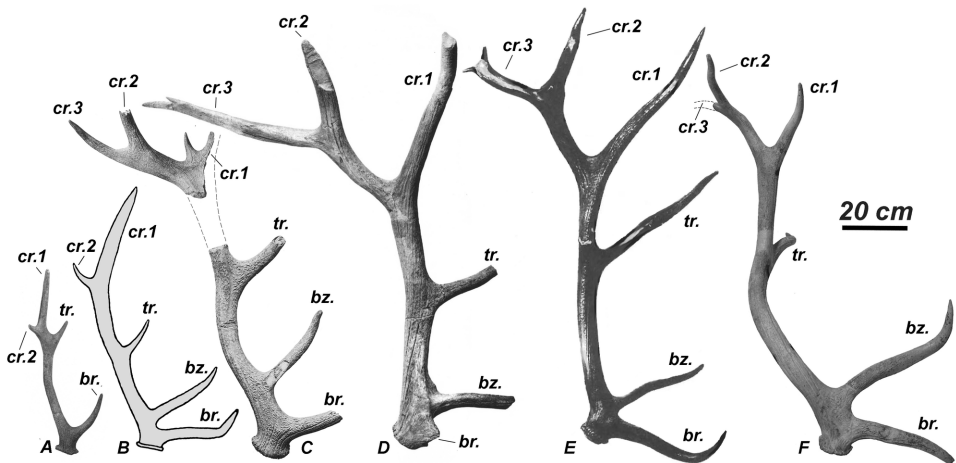


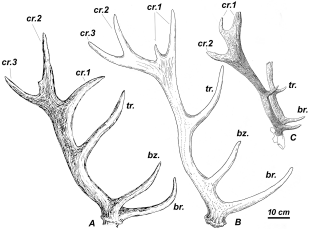










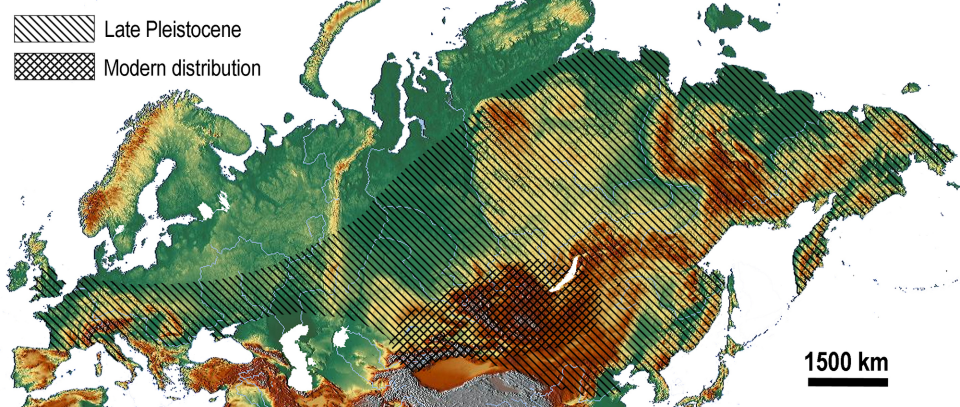




Late Pleistocene



Modern distribution



1500 km

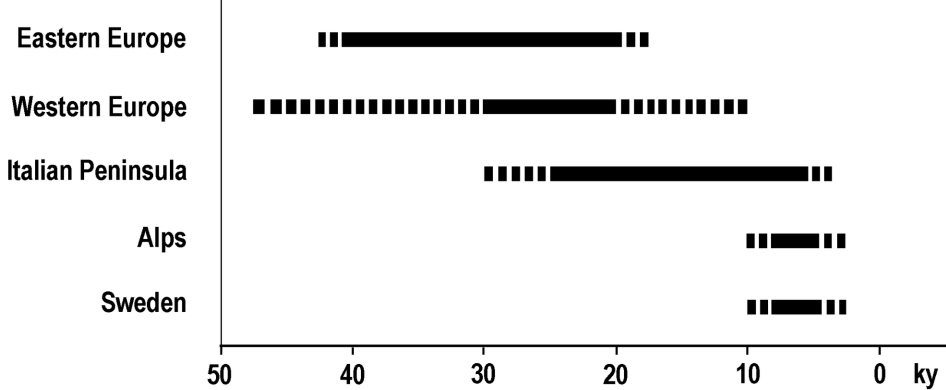


Table 1. *Cervus canadensis combrayicus* n. ssp., cranial measurements (mm) of the holotype compared to fossil wapiti *C. canadensis cherskii* from northeast Asia (adapted from Boeskorov, 2005).

Measurement	<i>C. c.</i> <i>combrayicus</i> , Saint-Hippolyte	<i>C. c.</i> <i>cherskii</i> , Nr. 105	<i>C. c.</i> <i>cherskii</i> , Great Lyakhovsky Island	<i>C. c.</i> <i>cherskii</i> , Nr. 2192
Frontal breadth	147.0			
Breadth behind pedicles	119.0			
Breadth of occiput	157.8	170.0	172.0	176.0
Breadth of occipital condyles	90.3			
Distance bregma- opisthocranion	105.0			
Occipital height (basion-opisthoranion)	108.2	102.0	106.0	107.8
Opisthion- opisthocranion distance	65.5	69.0		71.0
Height of foramen magnum	43.4			
Breadth of foramen magnum	35.1			
Lambda-opistocranion distance	38.7			
Distance between lateral points of pedicles	195.0			
Distance between supraorbital foramina	93.9			

Table 2. *Cervus canadensis combrayicus* n. ssp., measurements (mm) of pedicles and antlers of the holotype compared to *C. canadensis mongoliae* from the Quaternary of China (adapted from Zdansky, 1925) and *C. canadensis cherskii* from the Late Pleistocene of northeast Asia (adapted from Boeskorov, 2005).

Measurement	<i>C. canadensis combrayicus</i>		<i>C. canadensis mongoliae</i>	<i>C. canadensis cherskii</i> (holotype)
	right	left		
L antler		1140	1090	1235
H pedicle	34.5	36.8		
DAP pedicle	62.1	61.2		
DLM pedicle	60.7	61.8		
DAP burr	80.0	80.3	81.0	
DLM burr	76.7	78.2		
CF pedicle	188.0	190.0		
DLM above burr	54.7	59.8		
DAP above burr	70.3	73.2	74.0	
CF above burr	217.0	223.0		255
H brow tine ramification	96.5	92.0	72.0	
L brow tine	ca. 260	ca. 260		440
DLM brow tine base	45.5	41.0		
DAP brow tine base	31.4	29.8		
CF brow tine base	124.0	115.0		
H bez tine ramification	147.7	195.3		
L bez tine	ca. 315	ca. 390	> 162	
DLM bez tine base	40.1	44.3		
DAP bez tine base	37.2	37.3		
CF bez tine	125.0	131.0		
L between bez and trez ramifications	430.0	490.0	235.0	395

DLM beam between bez and trez ramifications	48.3	47.8		
DAP beam between bez and trez ramifications	51.4	50.0		
CF beam between bez and trez ramifications	160.0	160.0		190
L trez tine	126.0	> 180	> 132	
DLM trez tine	27.6	28.8		
DAP trez tine	36.2	36.0		
L between trez and 1 st crown ramifications		265.0	250.0	
DLM beam between trez and 1 st crown ramifications	49.0	48.0		
DAP beam between trez and 1 st crown ramifications	47.5	50.0		
CF beam between trez and 1 st crown ramifications	152.0	159.0		
L 1 st crown tine		218.0		
DLM 1 st crown tine		31.1		
DAP 1 st crown tine		36.3		
CF 1 st crown tine		116.0		
L between 1 st and 2 nd crown ramifications		180.0	192.0	

DLM beam between 1 st and 2 nd crown ramifications		30.7		
DAP beam between 1 st and 2 nd crown ramifications		45.0		
CF beam between 1 st and 2 nd crown ramifications		120.		
L 2 nd crown tine		> 160		
DLM 2 nd crown tine		24.5		
DAP 2 nd crown tine		28.2		
CF 2 nd crown tine		87.0		