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From continents to islands: tracking the red deer (*Cervus elaphus* Linnaeus, 1758) and its "troublesome cousin", the wapiti (*Cervus canadensis* Erxleben, 1777), in Europe

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From continents to islands: tracking the red deer (*Cervus elaphus* Linnaeus, 1758) and its "troublesome cousin", the wapiti (*Cervus canadensis* Erxleben, 1777), in Europe

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ABSTRACT
Deer represent a distinctive family of ruminant herbivores that have evolved a flexible and opportunistic ecological and evolutionary strategy, enabling them to grow luxurious and resource-demanding antlers that are shed annually. The family Cervidae ranks among the most diverse modern taxonomic groups of herbivores, with even greater diversity in the geological past. This ecological flexibility and opportunism align deer closely with hominins. The relationship between cervids and hominins was crucial for hominin survival during glaciation phases and likely played a role in the colonization of the New World by Paleolithic humans. Studies on the taxonomy and systematics of fossil cervids continue to yield new discoveries and insights. Recent research has revealed that the natural history of the genus *Cervus* in Europe is more complex than previously thought. We suggest that earliest representative of the genus is the small-sized *Cervus nestii* (Azzaroli, 1947) n. comb. from the Early Pleistocene of Italy, characterized by simple four-pointed antlers lacking a bez tine. The onset of the Middle Pleistocene saw the emergence of the large-sized red deer, with subspecies exhibiting antlers featuring a bez tine but no crown, known as *Cervus elaphus acoronatus* Beninde, 1937. Subsequently, approximately 400 000 years ago, the "modern" *Cervus elaphus* Linnaeus, 1758 emerged, displaying high plasticity, diversification, and giving rise to several subspecies during the Late Pleistocene. Our recent revisions at a European scale have uncovered the presence of the wapiti, *Cervus canadensis* Erxleben, 1777, a species currently inhabiting North America and Asia. From Crimea to Sweden, several subspecies previously attributed to the red deer have been reinterpreted and associated with the wapiti.

KEY WORDS
Cervidae,
morphology,
Pleistocene biodiversity,
Holocene biodiversity.

RÉSUMÉ
*Des continents aux îles : suivre le cerf élaphe (*Cervus elaphus *Linnaeus, 1758) et son « cousin gênant », le wapiti (*Cervus canadensis *Erxleben, 1777) en Europe.*
Les cervidés représentent une famille particulière d'herbivores ruminants qui a développé une stratégie écologique et évolutive, flexible et opportuniste. Cela leur a permis de développer de grandes ramures de bois, qui tombent et repoussent chaque année et qui nécessitent donc beaucoup de ressources et d'énergie. La famille des cervidés est l'un des taxons d'herbivores actuels montrant la plus grande diversité, diversité encore plus forte au cours des époques géologiques anciennes. Cette flexibilité écologique et cet opportunisme rapprochent les cervidés des hominines. La relation entre les cervidés et les hominines a été cruciale pour la survie des seconds pendant les phases de glaciation et a probablement joué un rôle dans la colonisation du Nouveau Monde par les groupes humains du Paléolithique. Les études sur la taxonomie et la systématique des cervidés fossiles continuent d'apporter de nouvelles découvertes et de nouvelles idées. Des recherches récentes ont révélé que l'histoire naturelle du genre *Cervus* en Europe est plus complexe qu'on ne le pensait. Nous suggérons que le premier représentant du genre est le petit *Cervus nestii* (Azzaroli, 1947) n. comb. du Pléistocène inférieur d'Italie, caractérisé par des bois simples à quatre pointes dépourvus de sur-andouiller. Le début du Pléistocène moyen a vu l'émergence du cerf de grande taille, avec des sous-espèces présentant des bois munis de sur-andouiller mais sans couronne, connues sous le nom de *Cervus elaphus acoronatus* Beninde, 1937. Par la suite, il y a environ 400 000 ans, le *Cervus elaphus* Linnaeus, 1758 « moderne » est apparu, faisant preuve d'une grande plasticité et d'une grande diversification, et donnant naissance à plusieurs sous-espèces au cours du Pléistocène supérieur. Par une révision récente des données à l'échelle européenne nous proposons l'identification du wapiti, *Cervus canadensis* Erxleben, 1777, une espèce qui habite actuellement l'Amérique du Nord et l'Asie. De la Crimée à la Suède, plusieurs sous-espèces précédemment attribuées au cerf élaphe ont été réinterprétées et associées au wapiti.

MOTS CLÉS
Cervidae,
morphologie,
biodiversité pléistocène,
biodiversité holocène.

INTRODUCTION

Deer (family Cervidae) are one of the most diverse modern groups of ruminant herbivores, distinguished by their unique cranial appendages. Unlike other ruminants, these appendages, known as antlers, become inert bony structures at the end of their biological cycle. The evolution and characteristics of antlers have fundamentally shaped the evolution, ecology, geographical distribution, relationships with other herbivorous mammals, and interactions with humans. To understand these features and relationships, it is essential to comprehend the biological advantages and constraints that antlers confer.

With few exceptions, antlers develop only in males and, depending on the species, may serve multiple functions. Primarily, antlers function as weapons during male-male competition for breeding opportunities, establishing hierarchies among males and playing a crucial role in sexual selection (Goss 1983; Geist 1998). A secondary function derived from this is visual communication, including conveying information about the health status and social standing of the male individual. In highly specialized cases, such as in giant deer with large palmated antlers, visual communication may outweigh the intraspecific fighting function. While antlers exhibit considerable variability, their function as organs of communication remains a crucial factor in preventing interbreeding between species. This is because the visual signals conveyed by antlers are species- or even subspecies-specific (Geist 1998).

Additional functions of antlers include protective roles provided by their ramification, such as fixing rivals' antlers, defense against predators, and the thermoregulatory function of growing antlers, which are rich in blood vessels and covered by skin (Stonehouse 1968; Goss 1983; Lister 1987a, Geist 1998; Croitor 2020a). Exceptions among cervids include reindeer (*Rangifer tarandus* (Linnaeus, 1758)), as both males and females possess antlers, and Chinese water deer (*Hydropotes inermis* Swinhoe, 1870), whose males have lost their antlers (Flerov 1952).

The development of antlers in female reindeer represents an adaptation, allowing females to defend the snow pits they dig to access lichens hidden beneath the snow from larger, stronger males (Tarasov 1956). Hence, antler shedding in reindeer males and females occurs asynchronously: males shed their antlers soon after the rutting season, while females shed theirs during springtime (Flerov 1952; Sokolov 1959). In *Hydropotes*, the function of antlers as an offensive rutting weapon is entirely replaced by very large saber-shaped upper tusks that attain 8 cm in length.

Male deer undergo annual cycles of antler growth and shedding, a unique evolutionary trait among mammals that entails significant energetic costs. The developing antlers are covered with vascularized skin, the "velvet", which covers the cartilaginous growing antler until its ossification, after which the skin is discarded and shed (Goss 1983). This process necessitates access to abundant, high-quality food resources rich in minerals and proteins. Such physiological specialization and dietary requirements serve as the cornerstone of cervid ecological opportunism and adaptability, representing an optimal

strategy for obtaining highly nutritious food. In addition to their preference for highly nutritious plant parts, cervids have also been observed occasionally consuming small vertebrates, bird eggs, and gnawing bones and shed antlers to acquire proteins and minerals (Flerov 1952). This feeding opportunism significantly influences the ecological and evolutionary strategy of the family Cervidae and the principles of ecological resources partitioning within the family (Geist 1998).

The family Cervidae is characterized by a wide range of body masses, with the smallest species being the pudu (25 to 45 cm tall at the shoulder, weighing 6 to 15 kg) and the largest being the moose *Alces alces* (Linnaeus, 1758) (male: 2.30 m tall at the shoulder, weighing 630 kg) (Flerov 1952; Geist 1998). Since the craniodental morphology in cervids, compared to bovids, remains relatively unspecialized, the difference in body mass is likely the primary eco-physiological factor ensuring ecological niche partitioning among sympatric species (Lister 1987a). The paleodiet analysis and frequency of cervid species that come from the same faunas show that body mass does not have a decisive influence upon forage choice, but rather influence the selection of habitats (Kaiser & Croitor 2004). This is the reason why we practically never find in the same fauna modern cervid species with similar body size. The term "fauna" is applied to fossil communities somehow arbitrarily. However, in the same way as in modern faunas, it is rare to find cervid species with similar body sizes and comparable frequencies of remains within the same fossil assemblage (Heintz 1970; Lister 1999; Croitor & Bonifay 2001).

Modern roe deer of the genus *Capreolus* exemplify adaptations to specific ecological niches for small-sized deer in temperate climates with pronounced seasonality. The two extant species, *Capreolus capreolus* (Linnaeus, 1758) and *Capreolus pygargus* Pallas, 1771, typically weigh around 35-40 kg and 55-60 kg, respectively (Flerov 1952). Throughout their range, they coexist with larger cervids such as *Cervus elaphus* Linnaeus, 1758, *Cervus canadensis* Erxleben, 1777, *Cervus nippon* Temminck, 1836, *Dama dama* (Linnaeus, 1758), and *Alces alces*. The relatively small body size of roe deer is an adaptation to the niche of small-sized ruminants in the mid-latitudes of Eurasia (Geist 1998). This specialization necessitates additional biological adaptations, such as prolonged gestation, to align their reproductive cycle with the seasonal patterns of these regions (Geist 1998). The evolutionary significance of body size reduction in continental *Capreolus* as an adaptation to resource partitioning among larger cervids is highlighted by the evolution of *Capreolus* in the conditions of insular isolation. *Capreolus miyakoensis* Hasegawa, Ōtsuka & Nohara, 1973 from the Late Pleistocene of Miyako Island attained a larger body size comparable to that of modern sika deer (Takakuwa *et al.* 1999). This increase in size in the insular roe deer from Japan is an unusual evolutionary trend for cervids under insular isolation. Typically, according to the "island rule", cervid lineages in isolated insular environments, absent terrestrial predators, tend to reduce their body size and develop "paedomorphic" cranial features (Sondaar 1977). However, *C. miyakoensis*, which did not face direct competition from larger deer, evolved to a body size comparable to fallow and sika deer. The potential influence of carnivores on the evolution of *C. miyakoensis*' body size can be dismissed, as the insular fauna included only a single predator, a small-sized cat (Oshiro & Nogara 2000).

Although the idea about body size difference as an ecological partitioning adaptation among sympatric cervid species was not explicitly explained, the size difference in teeth and postcranial bones remains reliable and broadly used method of separation of remains of sympatric species or species that come from the same fossil fauna (Zdansky 1925; Heintz 1970; Lister 1999).

Cervids exhibit limited ecological competitiveness compared to bovids, the latter being highly specialized for narrower and well-defined ecological niches with sophisticated eco-morphological adaptations facilitating the exploitation of resources and ecological partitioning among herbivore species (Spencer 1995; Geist 1998). The advanced eco-morphological specialization observed in African bovids, and other Afrotropical herbivores serves as the cornerstone guiding the establishment and functioning of the diverse herbivore communities within the stable ecosystems of Africa (Spencer 1995).

The limited ecological competitiveness of cervids, particularly in comparison to bovids, explains their inability to establish themselves within the African continent, dominated by diverse herbivore communities largely comprised of bovid species (Geist 1998). The endemic species *Megaceroides algericus* (Lydekker, 1890) represents an exceptional instance of cervid dispersal into Africa, likely taking place during a glacial phase that destabilized the Afrotropical ecosystems in North Africa. African endemic deer species persisted until the early Holocene, evolving extreme craniodental adaptations within a marginal ecological niche inaccessible to bovids: the periaquatic habitat, providing soft aquatic plants as a mineral-rich food source (Croitor 2016).

In the Palearctic region, which has experienced significant climate fluctuations over the past few million years, cervids have had a distinct advantage over bovids. Palearctic bovids predominantly occupy ecological niches characterized by relatively limited resources but maintain stability through various climate changes. These niches include mountainous and alpine ecosystems, as well as desert and semi-desert areas (Sokolov 1959; Crégut-Bonnoure 2007). During the Pleistocene, the evolutionary diversity of bovids in the Palearctic region became relatively restricted compared to the Ethiopian and Oriental zoogeographic areas. This diversity is mainly seen in the subfamily Caprinae, which underwent extensive evolutionary radiation in the mountainous areas of Eurasia, regions that remained largely inaccessible to cervids (Simpson 1945; Sokolov 1959; Geist 1987; Crégut-Bonnoure 2006, 2020).

Deer excel as good colonizers of newly available habitats in young emerging ecosystems devoid of competition from other large herbivores, readily switching between food resources provided they offer sufficient nutritional value (Geist 1998). This physiological trait has profoundly influenced cervid morphology, evolution, and biogeography. Consequently, cervids typically exhibit low craniodental specialization, primarily maintaining primitive brachyodont dentition (Flerov 1952). Cervids did not evolve advanced hypsodont teeth due to their feeding habits, which primarily involve nutrient-rich and soft plant parts. This physiological requirement for high-quality, abundant forage

diminishes the ecological competitiveness of cervids, particularly in the presence of bovid competitors (Geist 1998).

Cervids achieved notable success in colonizing North and South America, regions characterized by a very poor diversity of large herbivores during the Pliocene (Geist 1998; Webb 2000). In these regions, they underwent a prolific secondary evolutionary radiation comparable to the diversified early evolutionary radiations in the Old World (Geist 1998; Webb 2000; Croitor 2022). Cervids are among the few large herbivore groups that effectively exploited newly available territories following glacial retreats (Geist 1998; Meiri *et al.* 2013; Croitor 2022). Additionally, they have demonstrated remarkable adaptability to conditions of insular isolation (Caloi & Palombo 1995).

Thus, the highly diverse deer, with their large, branched, and often bizarre antlers, were among the first exotic animals encountered by ancient humans during their out-of-Africa journey. Despite evolving in different biogeographic contexts, deer and humans shared a common trait: ecological opportunism and the ability to colonize new territories and ecosystems. These shared characteristics facilitated a close relationship between human societies and deer.

Among the most evolutionarily specialized members of the family Cervidae, the reindeer (*Rangifer tarandus*) has developed exceptional adaptations to the cold Arctic climate (Flerov 1952; Tarasov 1956). Reindeer played a crucial role in human dispersals into high periglacial latitudes and significantly contributed to the survival of human populations in Europe during glacial phases (Bouchud 1966). It is conceivable that reindeer were an important resource that enabled Paleolithic humans to colonize America. Notably, reindeer remains the only domesticated deer species.

Although there have been relatively recent attempts to domesticate the moose (*Alces alces*) and employ it as draft animals, these efforts have failed due to several constraints imposed by cervid physiological requirements (Sokolov 1959). Firstly, deer require high-quality and nutrient-rich forage, rendering them economically less advantageous than the less demanding domesticated bovids (*Bos taurus* Linnaeus, 1758, *Ovis aries* Linnaeus, 1758, *Capra hircus* Linnaeus, 1758). Secondly, the attempts to utilize moose as draft animals failed because they were not sufficiently hardy and often died from overheating (Sokolov 1959). Nonetheless, deer have remained an important game species throughout prehistoric and historical times.

The true Cervidae have been documented since the Early Miocene, with genera such as *Procervulus*, *Dicrocerus*, *Acteocemas*, *Euprox*, and *Amphiprox* (Vislobokova 1990). The evolutionary radiation of the modern subfamilies Cervinae and Capreolinae occurred during the Late Miocene in two distinct zoogeographic areas of Eurasia: Southeastern Asia and Europe, respectively (Croitor 2022). The Late Miocene evolutionary radiation of capreolines was as diverse as the radiation of cervines, encompassing taxa which exhibit morphological convergence with some modern Eurasian cervines and extinct South American deer species (Croitor 2021, 2022). However, the taxonomic diversity of European capreolines was significantly reduced by numerous extinctions by the end of the Miocene (Croitor 2021). Today, they are represented by highly evolved species occupying ecological niches that are rather extreme for cervids (Geist 1998).

The subfamily Cervinae remains diverse and relatively intact to the present day, encompassing a range of modern species that exhibit varying degrees of evolutionary specialization, from the small-sized tropical *Muntiacus* and *Elaphodus* to the very large *C. canadensis*, which displays advanced adaptations to the comparatively cold Holarctic climate (Geist 1998). The genus *Cervus* is distributed throughout the entire Palearctic region and includes three modern species: the red deer (*C. elaphus*) in Western Eurasia and Central Asia, the wapiti (*C. canadensis*) in Siberia and mountainous regions of East Asia, and the sika deer (*Cervus nippon*) in Eastern Asia. Recent evidence suggests that the Atlas red deer from North Africa is the result of artificial introduction of European red deer by humans (Doan *et al.* 2017).

The paleontological record of the genus *Cervus* in Western Eurasia begins after the important *Pachycrocuta brevirostris* Aymard, 1846 event (sensu Martínez-Navarro 2010) –also known as the "Wolf event" (Azzaroli 1983)– which designates the decline of archaic warm-loving faunas containing many Pliocene holdovers, but also marked the first confirmed presence of hominins in Eurasia (Martínez-Navarro 2010). Despite numerous publications on the evolution, paleoecology, and diversity of *Cervus* in Europe, gaps remain in our understanding of the natural history of this genus. This paper aims to provide a comprehensive bibliographic overview of the available information on the diversity and evolution of the genus *Cervus* in Western Eurasia and to highlight areas where further research is needed to fill these gaps in our knowledge about red deer and its relatives in Europe.

ORIGIN AND DIVERSITY OF THE GENUS *CERVUS*

Cervus is the most successful modern genus of cervids, boasting an extremely vast distribution across Eurasia and North America. Nevertheless, *Cervus* retains many primitive features in its cranial morphology. The genus *Cervus* is characterized by a moderately flexed braincase (less than in *Dama*), relatively long pedicles that are somewhat divergent and inclined caudally, a narrow triangular basioccipital (similar to *Muntiacus* and *Rusa*), small upper canines, and long naso-premaxillary articulation (Heptner & Zalkin 1947; Flerov 1952). The cranial and dental specialized characters are few. The nasal bones are relatively long (longer than the upper tooth row), although they do not reach the line connecting the anterior edges of the orbits. Antlers of representatives of the genus *Cervus* are covered with a characteristic pearling (Averbouh 2016) or "perlation" (Goss 1983), making them easily distinguishable from most other cervid genera. The knobby appearance of the antler surface arises from the periosteum of growing antlers, which is responsible for the development of the pearling. The pearled antler surface is a specific morphological feature of the genus *Cervus* and some related forms that are sometimes also included in *Cervus*, such as *Rusa unicolor* (Kerr, 1792) and *Rusa timorensis* Blainville, 1822. Typically, antlers of the genus *Cervus* have four to five or more tines, including the brow tine (the evolutionarily oldest and most consistent element of *Cervus* antlers), the bez tine (an additional basal tine

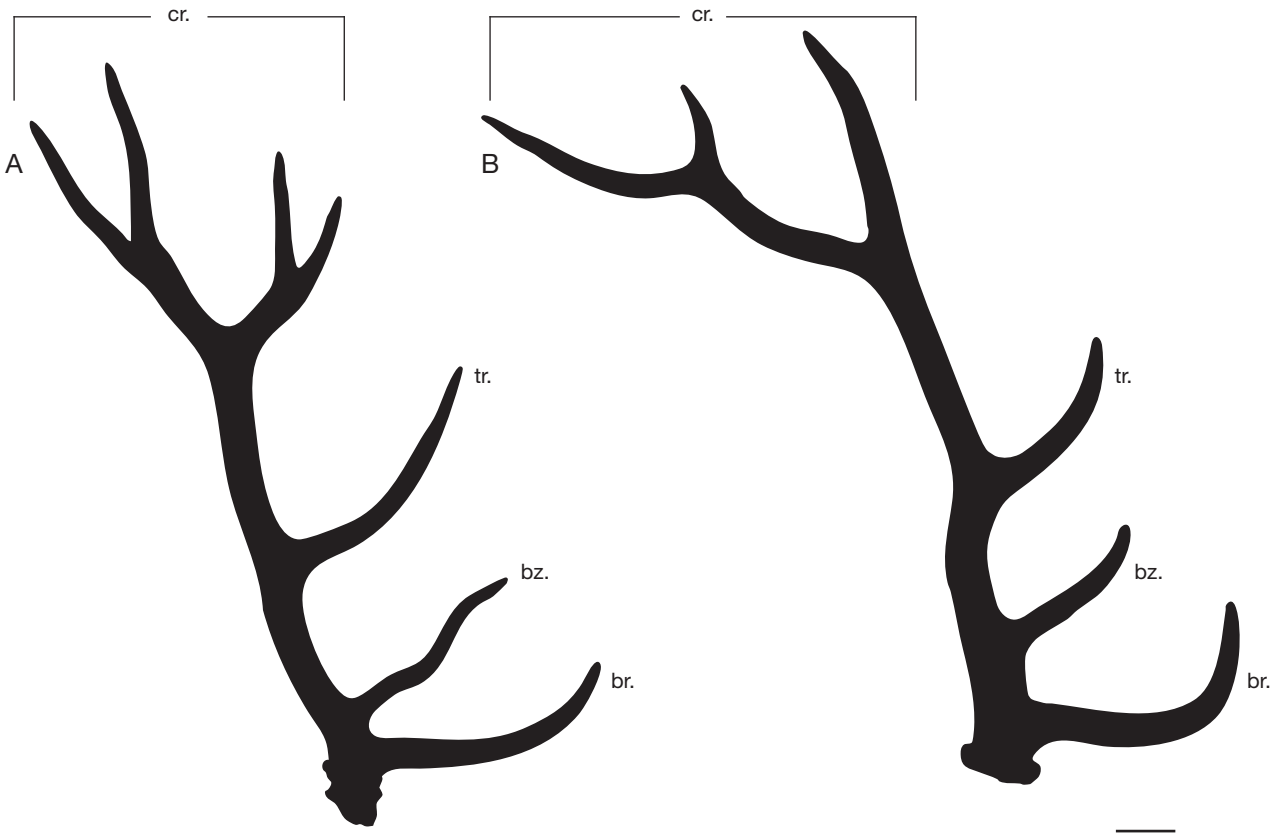

FIG. 1. — Antler shapes of *Cervus elaphus* Linnaeus, 1758 (**A**) and *Cervus canadensis* Erxleben, 1777 (**B**) with labeled terms for antler parts: **br**., brow tine; **bz**., bez tine; **cr**., antler crown; **tr**., trez tine. Scale bar: 10 cm.

seen in larger, more advanced species), the trez tine (or middle tine, corresponding to the anterior tine of the distal fork in *Rusa*), and distal crown tines, which emerged during the evolutionary transition to four- and five-tined antlers (Fig. 1).

The origin of the genus *Cervus* is linked to a deer form with three-pointed antlers similar to modern *Rusa*. The first appearance of a true representative of the genus, *Cervus magnus* (Zdansky, 1925) (= *Pseudaxis magnus* Zdansky, 1925), is reported from the beginning of the Early Pleistocene in China, dating back to around 2.6 million years ago. *Cervus magnus* represents the next step in antler evolution by developing an additional tine in the distal part of the antler. Its antlers 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 appears to be a homologue of the first crown tine in modern-type wapitis (Fig. 2A). According to Geist (1998) and Di Stefano & 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*. We rather consider that *C. magnus* is probably a direct precursor of *C. canadensis* and represents the evolutionary stage after the split of red deer and wapiti lineages (Croitor 2020a).

The lineage of European red deer is first recorded in the Early Pleistocene of Western Eurasia. Around 2 million years ago, *Cervus nestii* (Azzaroli, 1947) n. comb. (originally published as *Dama nestii* Azzaroli, 1947) with four-tined antlers emerges as the oldest European representative of the "*elaphus*" group (Kahlke 2001; Croitor 2006, 2011, 2018). It is found in Georgia (= *Cervus abesalomi* Kahlke, 2001; Dmanisi site, 1.8-1.76 million years old) as well as in Italy (Valdarno, Tuscany; probably between 2.0 and 1.3 million years ago; Olivola, approximately 2.1-1.9 million years ago: Croitor 2014).

The paleontological record of the earliest *Cervus* in Western Eurasia has been clouded by decades of taxonomic debate. A key role in understanding the early evolution of the *Cervus* lineage, which led to the modern red deer, is played by a small-sized deer with simple antlers from the Early Pleistocene of Italy. Azzaroli (1947) identified this cervid from the Upper Valdarno as *Dama nestii nestii* (Azzaroli, 1947), distinguishing it from *Dama nestii eurygonos* (Azzaroli, 1947) based on differences in distal antler bifurcation and other antler characteristics. Petronio (1979) later elevated both forms to species rank, citing their distinct morphological traits.

In 1992, Azzaroli reclassified *Dama nestii* Azzaroli, 1947 into the genus *Pseudodama*, describing *Dama eurygonos* (Azzaroli, 1947) as an "advanced form" of *Dama nestii*. The genus *Pseudodama* is poorly defined, primarily by helicoidal antler beams, and encompasses significant variability in traits such as dental morphology (presence or absence of a cingulum in upper molars, simple or molarized fourth lower premolars), pedicle shape and position (short and vertical *vs*. long and caudally sloped), braincase shape

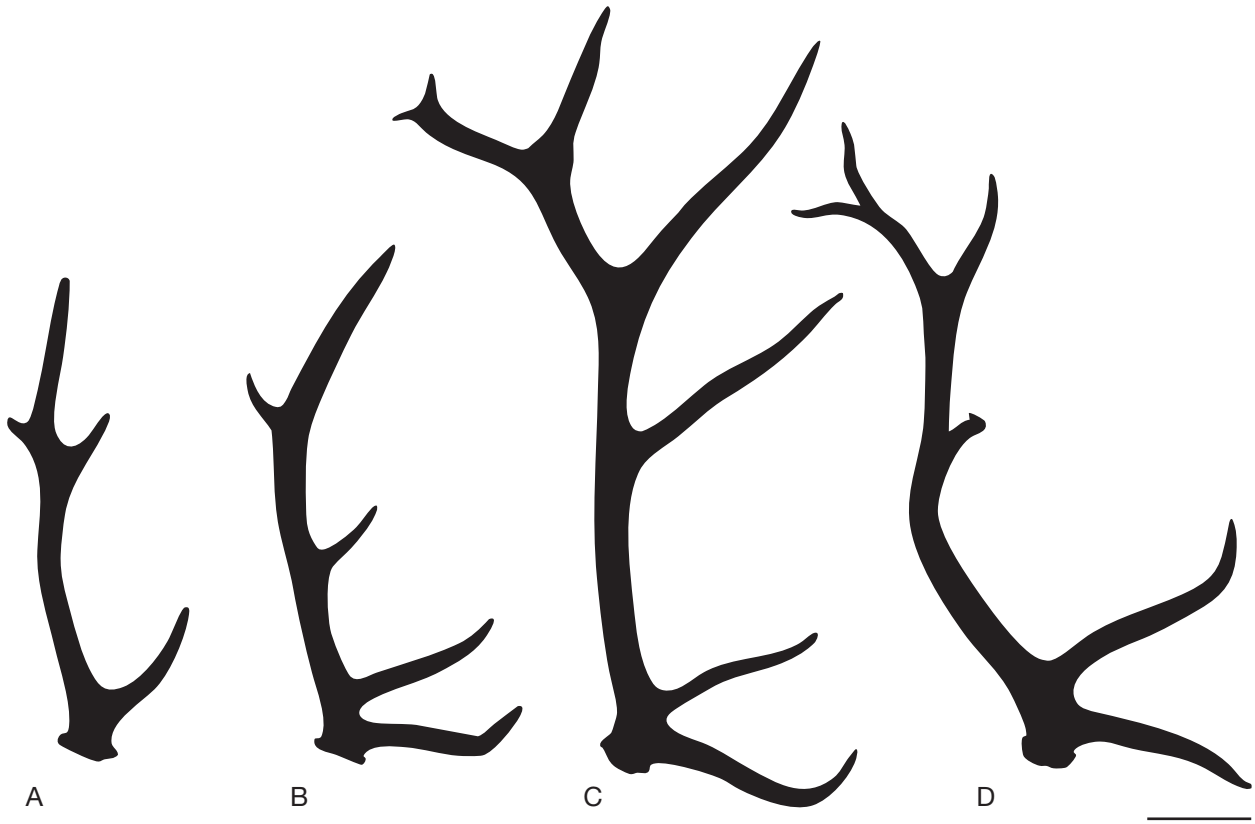

Fig. 2. — Antlers of Eurasian wapiti and wapiti-like deer: **A**, *Cervus magnus* (Zsansky, 1925) from the Early Pleistocene of China; **B**, antler of an extant MacNeill's stag *Cervus canadensis macneilli* Lyddeker, 1909; **C**, *Cervus canadensis cherskii* Boeskorov, 2005 from the Late Pleistocene of Siberia; **D**, *Cervus canadensis combrayicus* Croitor, 2020 from the Late Pleistocene of France, the median side of left antler. Credits: A, adapted (inverted image) from Zdansky 1925; B, adapted (inverted image) from Geist 1998; C, adapted from Boeskorov 2005; D, adapted from Croitor 2020a. Scale bar: 20 cm.

(slightly flexed with flat parietals *vs*. strongly flexed with convex parietals), and antler morphology (Croitor 2006). This taxonomic approach has generated extensive debate (Pfeifer 1997; Di Stefano & Petronio 1998, 2002; Croitor & Bonifay 2001; Croitor 2006; Petronio *et al.* 2013). Pfeifer (1997) suggested classifying *Pseudodama* as a subgenus within *Dama* based on postcranial bone morphology. However, this proposal remains controversial since it relies on limb bones unassociated with cranial or antler material. Additionally, many authors question the monophyly of *Pseudodama* (Di Stefano & Petronio 1998, 2002; Croitor & Bonifay 2001; Croitor 2006; Petronio *et al.* 2013).

Di Stefano & Petronio (2002) linked Villafranchian small-sized deer from Italy to modern Asian genera *Axis* and *Rusa* based on the general shape of three-pointed antlers. However, antler shape in this context reflects a universal evolutionary stage within Cervinae (Geist 1998) rather than a true phylogenetic relationship. Later, Petronio *et al.* (2013) placed Italian species in the genus *Axis*, interpreting them as advanced evolutionary stages. This classification is problematic, as *Cervus nestii* differs from *Axis axis* by its pronounced pearling, a trait shared with *C. elaphus* but absent in *Axis*. Furthermore, *Dama eurygonos* exhibits highly specialized cranial features, such as short, vertical pedicles and a rounded, flexed braincase (Croitor 2014).

Cranial morphology is a key tool in zoological systematics, providing insights into the systematic and phylogenetic relationships among species, including cervids (Flerov 1952; Vislobokova 1990; Croitor 2006). Analysis of cranial features in "*Dama*-like" deer –such as braincase shape and flexion, orbital position, nasal bone length, pedicle orientation, presence of upper canines, and ethmoidal opening shape– led us to suggest that *Pseudodama*'s genotype species, *Dama nestii nestii*, closely resembles the European red deer (*C. elaphus*) (Croitor 2006; Croitor & Robinson 2020). This affinity is supported by antler traits, including a pearled surface and the transverse distal fork orientation of four-tined antlers.

Hierarchical clustering of "*Dama*-like" deer with modern genera (*C. elaphus*, *Dama dama*, *Rusa unicolor*, and *Axis axis*) further supports these findings (Croitor & Robinson 2020). Results group *Dama nestii nestii* with *C. elaphus*, while *Dama eurygonos* aligns with modern fallow deer. Thus, we proposed that *Pseudodama* is a junior synonym for *Cervus*, and its type species should be reclassified as *Cervus nestii* (Croitor 2006; Croitor & Robinson 2020). Some authors (Breda & Lister 2013; Cherin *et al.* 2022) continue however to use the genus name *Pseudodama*.

Cervus nestii is a relatively small-sized deer with a body mass of approximately 60 kg. It has four-pointed antlers that terminate in a simple fork, oriented more or less transversely with respect to the body axis (Fig. 3A). This distinctive crown shape is shared by *C. nestii* with the earliest Middle Pleistocene

FIG. 3. — Antler bauplan of red deer and its Early Pleistocene small-sized relative, frontal view: **A**, *Cervus nestii* (Azzaroli, 1947) n. comb. (originally published as *Dama nestii* Azzaroli, 1947) from the Early Pleistocene of Upper Valdarno, Italy; **B**, *Cervus elaphus acoronatus* Beninde, 1937 from the Middle Pleistocene of Germany; **C**, *Cervus elaphus elaphus* Linnaeus, 1758 from the bogs of Ashkirk, Skotland. Credits: A, adapted from Azzaroli 1992; B, based on the specimen figured by Beninde 1937; C, adapted from Smith 1881. Scale bar: 10 cm.

red deer subspecies, *C. elaphus acoronatus* (Beninde, 1937), and the less evolved modern subspecies, *C. elaphus bactrianus* Lydekker, 1900, from Central Asia (Croitor 2006). The antler crown bauplan has important taxonomical significance in distinguishing between *C. elaphus* and *C. canadensis* (Beninde 1937; Flerov 1952; Sokolov 1959; Geist 1998). This difference in the pattern of the distal portion of the antler construction is already evident in *C. nestii* and *C. magnus.*

Therefore, the difference in construction and development of the 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. The third modern species, *Cervus nippon*, represents the four-point antler evolutionary stage like *C. magnus* and, according to mitochondrial DNA analysis, shows a closer phylogenetic relationship with *C. canadensis* than with *C. elaphus* (Kuwayama & Ozawa 2000; Pitra *et al.* 2004; Ludt *et al.* 2004).

The early evolutionary split of the *magnus-canadensis* and *nestii-elaphus* lineages prompts the question of how red deer and wapiti acquired the second proximal tine of their antlers, known as the bez tine. The most plausible explanation is that there was genetic exchange between these two lineages, a phenomenon commonly observed in the animal world (Arnold 2015). Multiple cases of such interspecific gene exchange within the *Cervus* lineage were reported by Hu *et al.* (2019). It appears that the small homology of the bez tine is also found in some specimens of modern *Rusa unicolor*, as seen, for instance, in the antlers of this deer figured by Cuvier (1823: pl. 5, figs 59, 60).

RED DEER *CERVUS ELAPHUS*

Cervus elaphus is a relatively old, highly successful, and adaptable species, primarily thriving in broadleaf forest biomes across the middle latitudes of western Eurasia (Geist 1998; Di Stephano & Petronio 2021). Several distinctive cranial features distinguish this species. The facial portion of the skull in largest subspecies (as, for instance, in *C. elaphus maral* Ogilby, 1840), is elongated, primarily due to the lengthening of the orbitofrontal portion, with the anterior edge of the orbit projecting behind the posterior edge of the upper third molar, M3 (Ogilby 1840). The lower mandible also displays elongated characteristics: its diastemal part is relatively long and attains from 63.0 % to 82.5 % of the lower toothrow length, the angle between the horizontal and ascending ramuses is more open compared to other deer species, and the processus angularis is poorly pronounced. The lower fourth premolar typically exhibits molarization, although this trait can vary.

The earliest fossil records of red deer date back to the early Middle Pleistocene of Europe, around 900 000 years ago. The earliest red deer, described as subspecies *C. elaphus acoronatus*, is characterized by the development of a simple distal fork and a very strong and long bez tine (Figs 3B, 4A). This subspecies is one of the largest forms of red deer, with an average weight estimated at *c.* 240 kg. It has been identified in England, Germany (including remains of young individuals reported as *Cervus elaphoides* Kahlke, 1960, and *Cervus reichenaui* Kahlke, 1996), France, Italy, the Netherlands, and Moldova (Beninde 1937; Lister 1990; Di Stefano & Petronio 1992). The early acoronate red deer evolved into several specialized endemic European subspecies, characterized by further complication of antler crown or specific evolutionary specializations in the case of Mediterranean dwarfed forms (Beninde 1937; Azzaroli 1961; Di Stephano & Petronio 2021).

Between 600 000 and 500 000 years ago, European red deer began to evolve a multiaxial antler crown. The initial simple antler crown consisted of three tines. This evolutionary stage of red deer was identified as *C. elaphus antiqui* Pohlig, 1892. In France, evidence of early crowned deer dates back to around 400 000 years ago at the site of La Caune de l'Arago (Pyrénées Orientales) (Magniez *et al.* 2013).

The evolution of *C. elaphus angulatus* Beninde, 1937 (occurring at the end of the Middle Pleistocene in Germany, approximately 250 000 years ago) is marked by further complication of the distal portion of the antler. The primary evolutionary development of *C. elaphus angulatus* is the emergence of a third

extremely hypermorphous posterior crown tine, in addition to a transversal fork (Fig. 4B). This additional tine is directed backward and forms an angle with the antler beam, often flattens and bears additional digitations. This peculiar variant of antlers with flattened distal portion instead of multiaxial crown is still present in some modern red deer populations of Western Europe (Johnston 1903).

Several endemic subspecies have been documented from the Pleistocene of Italy. *C. elaphus rianensis* Leonardi & Petronio, 1974 (also known as *C. elaphus eostephanoceros* Di Stefano & Petronio, 1993), from the end of the Middle Pleistocene of the Italian Peninsula, is distinguished by a reduction in body size (with an estimated body mass of approximately 100 kg) and a significant shortening of the distal portion of antlers terminating in a simple fork, similar to *C. elaphus acoronatus*.

C. elaphus siciliae Pohlig, 1893 (occurring at the end of the Middle Pleistocene and Upper Pleistocene of Sicily) was an endemic dwarfed insular red deer with an estimated body mass of approximately 60 kg (Gliozzi *et al.* 1993). The dwarfing of body size resulted in disproportionately broad frontal bones, a relatively narrow occiput, and noticeably divergent antlers. Some specimens are characterized by a three-tined crown, suggesting that *C. elaphus siciliae* evolved from *C. elaphus antiqui* or a similar form.

C. elaphus jerseyensis Zeuner, 1940 represents a unique case of strong evolutionary specialization of red deer in the conditions of insular isolation on the northern island of Jersey in the English Channel (Zeuner 1946; Lister 1989). This dwarfed form of red deer evolved during the last interglacial period (Eemian = MIS 5e) and underwent a rapid six-fold reduction in body size to approximately 36 kg (Lister 1989). As a result, *C. elaphus jerseyensis* reached a size comparable to that of roe deer. It is the smallest form of red deer, with antlers that retained their trez (middle) tine and only one basal tine positioned at a certain distance from the burr (Zeuner 1946).

In France, a small-sized deer with teeth exhibiting a more primitive structure compared to other fossil deer populations has been identified in several archaeological levels with Mousterian industry (Layers 54 to 50A; MIS 5) at the Combe-Grenal shelter (Dordogne, Western France). This deer is referred to as *Cervus simplicidens* Guadelli, 1997. However, this taxon has been invalidated because the species name had already been used by Lydekker (1876). Furthermore, the particular morphological characteristics of the teeth, such as primitive unmolarized lower fourth premolar, are occasionally observed in other populations of *C. elaphus* (Janis & Lister 1985). The origin of small-sized red deer from Dordogne is most probably related to the Iberian glacial refugium, and further investigation is needed to determine its possible relationship with modern *C. elaphus hispanicus* Hilzheimer, 1909 (= *C. elaphus bolivari* Cabrera, 1914), a smaller red deer subspecies from the Iberian Peninsula (Cabrera 1914).

Today, the red deer is represented by several subspecies and forms. The hypothesized area of its origin is the Tarim region in China (Ludt *et al.* 2004). Among the modern subspecies, the Bactrian deer (*C. elaphus bactrianus*) is one of the forms that retains the most primitive characteristics, inhabiting riparian forests of Central Asia. This subspecies is characterized by antlers that feature a bez tine and terminate in a simple transverse distal fork, typically exhibiting a total of six antler tines. According to some reports, primitive white spotting on their backs is retained even in some adults (Flerov 1952).

Taxonomic interpretations based on mitochondrial cytochrome *b* and control region marker analyses of primitive red deer subspecies (Lorenzini & Garofalo 2015), merit closer examination. Lorenzini & Garofalo (2015) concluded that Central Asian red deer subspecies are genetically distinct from their Western counterparts, forming a regional monophyletic group. They proposed classifying this group as a separate species, *Cervus hanglu* Wagner, 1844, comprising the subspecies *hanglu*, *bactrianus*, and *yarkandensis*.

However, this genetic study, which sought to redefine the taxonomic status of red deer subspecies, notably did not include type specimens in its analysis. Additionally, Lorenzini & Garofalo (2015) acknowledged that their findings do not align with the morphology-based subspecific taxonomy within *C. elaphus*. Despite this discrepancy, they failed to provide revised diagnoses for the taxa whose statuses were altered. This tripartite classification of elaphines (*C. elaphus*, *C. hanglu*, and *C. canadensis*) has since been adopted by other researchers (e.g., Meiri *et al.* 2018). In our opinion, the elevation of *C. elaphus hanglu* to species rank appears to have been driven more by conservation objectives (Lorenzini & Garofalo 2015; Narayan *et al.* 2024) than by strict adherence to established taxonomic principles and criteria.

Lorenzini & Garofalo (2015) classified Central Asian red deer as a distinct species, *Cervus hanglu*, citing genetic distances from Western red deer subspecies comparable to those between *C. canadensis* and *Cervus nippon*. However, to date this classification still has some important gaps. Their interpretations do not align with the biological species concept (Mayr 1942), which emphasizes genetic isolation, nor with the ecological species concept (Van Valen 1976). According to Van Valen, a species is defined by its occupation of a distinct adaptive zone and its evolutionary separation from other lineages. The classification proposed by Lorenzini and Garofalo lacks consideration of whether *Cervus hanglu* occupies a unique ecological niche or exhibits diagnostic ecological adaptations, both of which are crucial to supporting its status as a distinct species under the ecological framework. Divergence time alone is not a sufficient criterion for taxonomic classification. Subspecies can remain isolated for extended glaciation periods, yet if environmental conditions remain stable and evolutionary rates are slow –such as in glacial refugia– they tend to retain conservative traits and remain subspecies. This type of natural selection in glacial refugia is actually an example of stabilizing selection. Modern Central Asian red deer exhibit traits more consistent with the oldest known red deer subspecies, *C. elaphus acoronatus*, rather than displaying unique adaptations to new ecological niches.

In contrast, the relatively recent divergence between *C. nippon* and *C. canadensis* illustrates rapid evolution within a new adaptive zone, driven by directional selection under extreme ecological and climatic pressures. This divergence resulted in

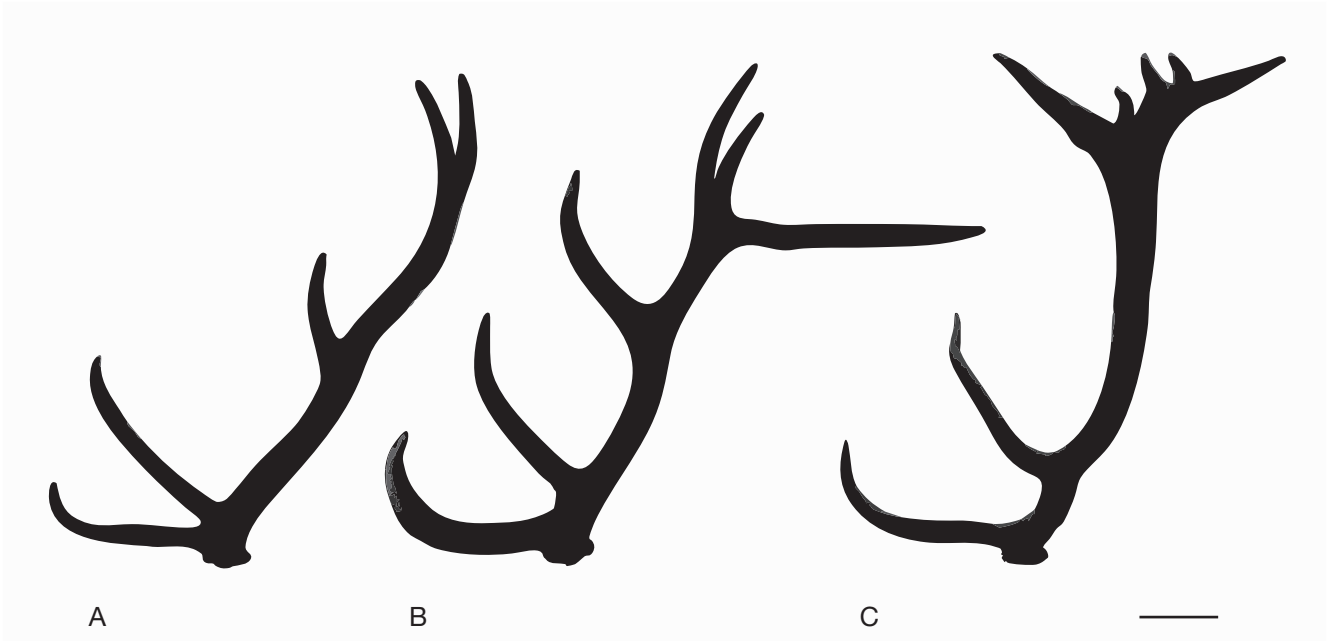

FIG. 4. — Side view of antlers of less specialized subspecies of red deer: **A**, *Cervus elaphus acoronatus* Beninde, 1937 from the Middle Pleistocene of Germany; **B**, *Cervus elaphus angulatus* Beninde, 1937 from the Middle Pleistocene of Germany; **C**, *Cervus elaphus maral* Ogilby, 1840 from the Late Pleistocene of Romania. Credits: A, adapted from Beninde 1937; B, Steinheim/Herr, Nr. 16201, the State Natural History Museum of Stuttgart; C, adapted from Croitor & Cojocaru 2016. Scale bar: 10 cm.

distinct morphological and biological adaptations to their respective niches, justifying their classification as separate species.

Based on these considerations, we still consider *C. elaphus bactrianus*, *C. elaphus yarkandensis* Blanford, 1892, and *C. elaphus hanglu* as a group of primitive subspecies within *C. elaphus*.

The Caspian red deer, *C. elaphus maral*, ranges from North Iran to the Carpathian region in Europe. This subspecies is the largest among red deer, characterized by several primitive features, including the frequent absence of the bez tine (Fig. 4C) and rudimentary white spots on the back, particularly notable in populations from the Caucasian area (Heptner & Zalkin 1947; Flerov 1952). The crown part of the antler exhibits a distinct pattern of complexity, which can be considered metameric: it consists of an axial tine with one or two to three transversal forks, resulting in a potential increase in the number of crown tines up to seven (Fig. 4C). This subspecies has been documented in the Balkan area since the Late Pleistocene and is likely closely related to the Late Pleistocene red deer subspecies *C. elaphus aretinus* Azzaroli, 1961 from the Italian Peninsula (Croitor & Cojocaru 2016).

The modern West European red deer, *C. elaphus elaphus* L., is distinguished by its highly evolved multiaxial cup-shaped crown and the consistent presence of the bez tine (Smith 1881; Lydekker 1898; Heptner & Zalkin 1947; Flerov 1952; Sokolov 1959; Geist 1998). The most basic form of an antler crown consists of an initial terminal transversal fork with an additional third tine emerging from the posterior side of the bifurcation base. As antler development progresses, it undergoes hypermorphosis characterized by the multiplication of terminal forks (Fig. 3C). In the most extreme cases observed in adult males, the terminal growth forms a cup-like structure composed of multiple tines in the crown (Smith 1881; Lydekker 1898; Johnston 1903; Beninde 1937; Heptner & Zalkin 1947; Flerov 1952). White spots on the back of adults have never been reported. This subspecies of red deer is considered the most evolved, with its origin traced back to the Iberian glacial refugium. Its current distribution expanded following the retreat of glaciers during the Holocene (Ludt *et al.* 2004; Meiri *et al.* 2013).

Other forms of red deer found in Western Europe have more restricted distributions and are often considered synonyms of the nominotypical subspecies *C. elaphus elaphus*. These include the Iberian red deer (*C. elaphus hispanicus*), the British red deer (*C. elaphus scoticus* Lönnberg, 1906), and the Norwegian red deer (*C. elaphus atlanticus* Lönnberg, 1906). These subspecies are characterized by smaller body size and simplified antlers, features that may represent clinal variation (Lönnberg 1906; Heptner & Zalkin 1947).

EURASIAN WAPITI *CERVUS CANADENSIS*

It took a considerable amount of time to accept the idea that the Canadian stag or wapiti constitutes a distinct species. There were however doubtless genetic, ecological, and biological evidence over the last several decades. This evidence failed to sway the conservative, oversimplified view on the taxonomy of *C. canadensis*, which was initially regarded as a group of subspecies of *C. elaphus*. Nonetheless, the history of discovery and exploration of this species is very long. In 1777, Erxleben introduced the binomial species name *C. canadensis* for the wapiti, though the exact characteristics of this deer, aside from its larger size, remained unclear. Schreber (1836) proposed a new species name for a large form of North American deer, *Cervus strongyloceros*, accom-

panied by a brief description and figures representing the pelage color of a female and a shed antler. In the same work, Schreber (1836) published a description of "*C. 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 to notice the striking resemblance between the Siberian *Cervus maral* Gray, 1860 (distinct from the name *C. elaphus maral* given to the Caspian red deer) and the North American *C. canadensis*. Lydekker regarded the wapiti as a true species, *C. canadensis*, and introduced the new subspecies name *C. canadensis asiaticus* Lydekker, 1898 for the Asian wapiti.

The "lumping" approach to the systematics of the "elaphine" deer (the species complex of *C. elaphus* and *C. canadensis*) dominated the zoological literature of the second half of the 20th century. American wapiti, Asian maral, and izubr stags were considered subspecies of the common red deer, *C. elaphus* (Heptner & Zalkin 1947; Ellerman & Morrison-Scott 1951; Flerov 1952; Sokolov 1959; Geist 1998). Heptner & Zalkin (1947) proposed that populations of Siberian wapiti in natural conditions are genetically isolated from Western and Central Asian red deer, although they noted that the areas of distribution of Asian wapitis and red deer forms never overlap, suggesting they are likely subspecies of the same species. The ease of hybridization between wapiti and red deer was also considered by Heptner & Zalkin (1947) as an argument for including various geographical elaphine forms as subspecies of the single species *C. elaphus*.

Flerov (1952) grouped Asian wapitis in the subspecies *C. elaphus canadensis* alongside North American wapitis. However, according to Sokolov (1959), the remarkable similarity in pelage coloring and antler shape of *C. elaphus sibiricus* and *C. elaphus canadensis* should be regarded as an evolutionary parallelism. He preferred to maintain these two elaphine forms as distinct subspecies of *C. elaphus*.

The caution in distinguishing red deer and wapiti as two independent species appears to stem from a lack of detailed morphological, biological, and ethological studies. Body size, the only readily available feature distinguishing red deer and wapiti, varies greatly within the better-known *C. elaphus* (Heptner & Zalkin 1947; Flerov 1952; Geist 1998). On the other hand, the simplified viewpoint on the taxonomy of red deer and wapiti has reduced scholars' interest in comparative morphological studies of these two species. Consequently, there is a dearth of comparative data on cranial and dental morphology between the two species. The only known morphological characteristics of wapiti pertain to antler shape, which is used in subspecies descriptions.

However, the reproductive isolation of wapiti and Western red deer populations in natural conditions are ensured by ethological, biological, and ecological differences (Heptner & Zalkin 1947; Geist 1998). Considering 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 true species *C. canadensis*, clearly distinct from red deer *C. elaphus*.

The reassessment of taxonomic criteria for "elaphine" deer came much later with genetic studies revealing significant phylogenetic distances between European red deer and Asian and American wapitis (Kuwayama & Ozawa 2000; Polziehn & Strobeck 2002; Ludt *et al.* 2004; Pitra *et al.* 2004). Molecular data reinstated the species status for *C. canadensis* (Polziehn & Strobeck 2002), further supported by ecological, physiological, ethological, and biological evidence, including semi-lethal hybridization between *C. canadensis* and *C. elaphus* (Schonewald 1994; Geist 1998; Croitor & Obada 2018).

In China, three subspecies are currently recognized: the Gansu wapiti (*C. canadensis kansuensis* Pocock, 1912), the Tibet and Bhutan wapiti (*C. canadensis wallichi* Cuvier, 1823), and the Sichuan wapiti (*C. canadensis macneilli* Lyddeker, 1909; Fig. 2B). These subspecies are distinguished by their relatively smaller antlers with less developed distal portions, often characterized by a simple fork (Cuvier 1823; Lydekker 1896; Pocock 1912; Geist 1998). The distinctions between subspecies primarily lie in the patterns and overall coloration of their pelage, including the shape and hue of the rump patch, which plays a role in social communication.

Four other subspecies are recognized, bringing the total number of Asian subspecies to seven: the Altai wapiti (*C. canadensis sibiricus* Lydekker, 1898), the Tien-Shan wapiti (*C. canadensis songaricus* Erxlerben, 1777), the Manchurian wapiti (*C. canadensis xanthopygus* Edwards, 1867), and the Ala-Shan wapiti (*C. canadensis alashanicus* Bobrinskii & Flerov, 1935). These subspecies are characterized by larger antlers with a strongly developed crown portion consisting of three tines, with the first crown tine being the longest and the strongest.

The most advanced evolutionary specializations are found in North American wapiti. Five subspecies exist in North America: the Roosevelt wapiti (*C. canadensis roosevelti* Merriam, 1897), the Tule wapiti (*C. canadensis nannodes* Merriam, 1905), the Manitoba wapiti (*C. canadensis manitobensis* Millais, 1915), and the Rocky Mountain wapiti (*C. canadensis nelsoni* Bailey, 1935). The southernmost subspecies of North American wapiti, *C. canadensis merriami* Nelson, 1902, which was characterized by a tendency to develop palmated antlers, is now extinct.

WAPITI IN THE PLEISTOCENE OF EUROPE

The notion of a deer similar to the modern North American wapiti existing in Europe during the Glacial epoch was closely tied to debates about the taxonomic status of the modern wapiti. These debates have a long history, dating back to Owen (1846), who described poorly represented fossil remains of an unusually large wapiti-like deer that rivaled the giant deer *Megaloceros giganteus* (Blumenbach, 1799) in size. Owen reported and illustrated an exceptionally large basal portion from Late Pleistocene deposits in Kent's Cavern, which resembled the morphology of the red deer but with dimensions approaching those of the largest modern North American wapiti. The antler fragment bore two basal tines (brow and bez) similar to those in modern red deer, with a circumference of the beam measuring 381 mm (15 inches) between the brow and bez tines, according

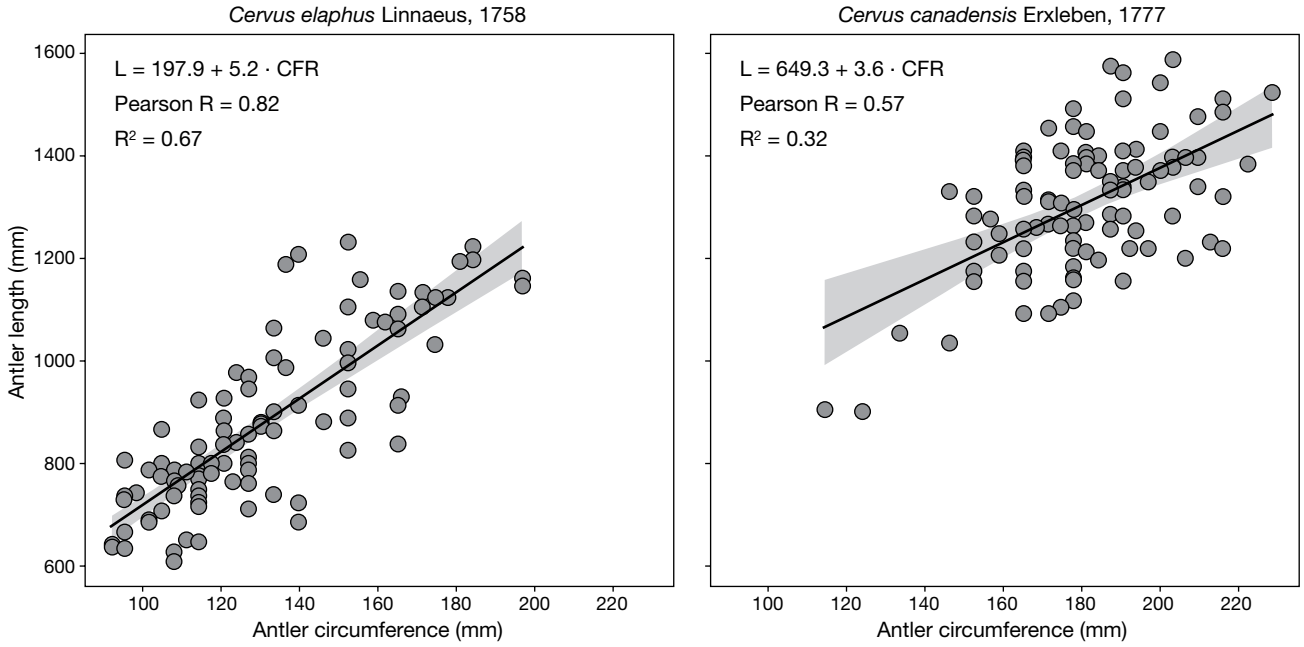

FIG. 5. — Linear regressions of antler length on antler beam circumference for modern *Cervus elaphus* Linnaeus, 1758 and *Cervus canadensis* Erxleben, 1777, with the 95 % Confidence Interval shown in gray. Data are adapted from Ward (1892). The exceptionally robust antlers of *Cervus canadensis* are excluded from the data used in the linear regression. Abbreviations: **CFR**, antler beam circumference; **L**, antler length; **R**, Pearson correlation coefficient.

to Owen (1846). The circumference of the type specimen above the burr was 375 mm, exceeding the analogous measurements of modern European red deer (*C. elaphus*), which range from 220 to 230 mm (Friant 1957). Owen (1846: 470) described the stag from Kent's Cavern as a new species placed within the subgenus *Strongyloceros*: *Cervus* (*Strongyloceros*) *spelaeus* Owen, 1846, meaning "the cave deer". Thus, for Owen (1846), the Canadian wapiti is identified as *Cervus* (*Strongyloceros*) *strongyloceros* Schreber, 1836, although he did not explicitly state this combination of subgenus and species name. Owen therefore assumed a close relationship between the new species from Kent's Cavern and the North American wapiti (*Cervus strongyloceros* and *C. canadensis*), suggesting that the British form may differ in the longer distance between the brow and bez tines. The remains of *Strongyloceros spelaeus* Owen, 1846 and associated fauna are from the Cave Earth layer (*terre de la caverne*; Friant 1957) dated to the Early to Middle Devensian Age, ranging from 100 000 to 30 000 years before the present (Lister 1987b).

The reports of wapiti from Paleolithic sites in Western Europe became quite frequent over the following decades. Thus, Pomel (1853) documented, under the name *Cervus intermedius* de Serres, 1838, some remains of a large deer resembling the American wapiti found at several fossiliferous sites in Auvergne (Central France). It appears that Pomel chose this species name under the assumption that the deer in question had an intermediary size between the red deer and the giant deer. However, the species name used by Pomel (1853) is not appropriate. *Cervus intermedius* was initially mentioned by de Serres (1838) in the fossil fauna list of the Middle Pleistocene site of the Lunel-Viel Cave and was reasonably considered by Boule (1892) as a junior synonym of *C. elaphus*. Pomel (1853) provided some diagnostic characteristics 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, similar to 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 among the sites where this cervid form was recorded.

Gervais (1861, 1872) documented the discovery of a large-sized *Cervus strongyloceros* from the Cave of Pontil near Saint-Pons (Hérault, Southern France) and the Cave of Loubeau near Melle (Haute-Garonne, Western France), both associated with a typical Late Pleistocene fauna. Rivière (1873, 1905) reported *C. canadensis* from the Paleolithic faunas of the Caverne du Cavillon near Menton (Alpes-Maritimes, Southern France) Menton and the Grotte de la Mouthe in Dordogne (Western France). Gaudry (1876) attributed cervid remains from Louverné in Mayenne (North-West France) to *C. canadensis*, including a basal fragment of a very large shed antler with brow and bez tines and an isolated large molar with a strong entostyle. In addition, Gaudry (1880) documented the discovery of wapiti from Laugerie-Basse (Dordogne, Western France) in association with abundant remains of a horse, reindeer, and saiga. De Rance (1888) reported *Strongyloceros spelaeus* from Cefn Cave (Wales, England) in association with Late Pleistocene fauna.

Belgrand (1883) described a proximal part of an antler with a pedicle, recovered from the sandpit of Grenelle in the Seine Valley, as *Cervus* (*canadensis*) (*sic*). He noted the exceptionally large size of the antler, with the pedicle circumference measuring 200 mm and the antler beam circumference above the bez tine measuring 210 mm. To assess the general size of Belgrand's specimen and compare it with available antler size data from the literature, we developed a linear regression model (Fig. 5)

TABLE 1. — Descriptive statistics for the total antler length and of hunting trophy antlers from red deer (*Cervus elaphus* Linnaeus, 1758) and North American wapiti (*Cervus canadensis* Erxleben, 1777). Antler measurements, adapted from Ward (1892), are presented in millimeters. Abbreviations: **CFR**, beam circumference above bez tine; **L**, total antler length; **Max**, maximum; **Min**, minimum; **Std**., standard deviation.

	Cervus elaphus		*Cervus canadensis*	
Statistic	**L**	**CFR**	**L**	**CFR**
Count	99	99	100	100
Mean	876.1	130.5	1309.6	186.7
Std.	164.6	25.9	132.3	32.3
Min	609.6	92.1	901.7	114.3
25 %	758.9	111.1	1219.2	170.7
50 %	838.2	127.0	1320.8	181.0
75 %	992.3	152.4	1397.0	197.7
Max	1231.9	196.9	1587.5	330.2

using measurements from modern *C. canadensis* specimens in North America, as reported by Ward (1892) (Table 1). The estimated total length of Belgrand's antler specimen is approximately 1407 mm. This places the antler from the Paris Basin among quite large specimens recorded for modern wapiti (Fig. 6). The bibliographic study presented here indicates that previous authors recognized the unusually large size of the antlers as a distinguishing feature of the reported fossils in comparison to common red deer and noted their association with periglacial fauna.

However, not all antlers from Western Europe reported as belonging to wapiti can be definitively attributed to this species. For instance, Martin (1893) described a basal fragment of an antler from the Bassin du Pignon (Hautes-Alpes, Southern France) as *C. canadensis* and provided measurements: the distance between the brow and bez tines was 23 mm, the maximal diameter of the beam between the bez and brow tines was 55 mm, and the minimum diameter of the same part of the beam was 40 mm. The approximately calculated circumference between the brow and bez tines is 150 mm, while the beam circumference above the bez tine is likely even smaller, placing the antler in question within the size variation observed in *C. elaphus*.

Nonetheless, De Stefano (1911) argued that the presence of *C. canadensis* in Europe, based on scant osteological remains, cannot be definitively proven. Lydekker (1915) expressed doubts regarding the presence of *C. canadensis* in the Late Pleistocene of Western Europe and considered *Strongyloceros spelaeus* as a junior synonym of *C. elaphus*, a viewpoint that gained general acceptance thereafter.

The Middle Pleistocene red deer subspecies *C. elaphus acoronatus*, with a body size comparable to modern wapiti, presents a significant challenge for researchers. Consequently, the exceptionally large remains of *Cervus* from the Late Pleistocene of Europe have often been interpreted as intraspecific variations of the red deer (Azzaroli 1961; Lister 1987a). While the presence of two distinct size forms of "elaphine" deer in the Late Pleistocene of Western Europe has been acknowledged (Prat & Suire 1971; Lister 1987a; Guadelli 1997), the taxonomical interpretation based on this size difference has been hindered by the absence of complete antlers preserving distal portions, which provide the primary diagnostic characters of "elaphine" deer species and subspecies (Lydekker 1896, 1898; Heptner & Zalkin 1947; Flerov 1952; Geist 1998). Consequently, the question of the occurrence of wapiti in the Late Pleistocene of Europe remained unresolved for more than a century.

The debate regarding the presence of large-sized elaphine deer in France was reignited by Friant (1952, 1957), who considered the giant cave stag from Kent's Cavern (= Kent's Hole) to be an exceptionally specialized elaphine deer. Friant (1952, 1957) proposed elevating Owen's *Strongyloceros* to full genus status and argued that the Pleistocene wapiti from Western Europe constituted a distinct species not identical to the European red deer. In addition to the antlers' considerable size, Friant (1952, 1957) pointed out diagnostic characteristics of *Strongyloceros spelaeus*, such as the oblique position of the antler base relative to the pedicle axis and the complete fusion of the radius and ulna.

It is noteworthy that Friant (1957) documented both *Strongyloceros spelaeus* and *C. elaphus* in the fauna of Kent's Cavern, which is not surprising given the extensive accumulation period of the fossiliferous layer. Friant (1957) also attributed to *S. spelaeus* the remains of a large-sized deer from Continental Europe described as *Cervus primigenius* Kaup, 1839. However, as she noted, the antlers of the continental large-sized stag remained unknown.

According to Lister (1987b), some specimens from Kent's Cavern attributed by Friant (1952, 1957) to *S. spelaeus* actually belong to *Megaloceros giganteus*: the palatal fragment 5646 with an upper tooth series exhibiting a relatively weak lingual cingulum in upper molars (Friant 1957: pl. 3, fig. 1), the left hemimandible Nr. 14.11.35 (Friant 1957: pl. 3, fig. 3) displaying well-expressed pachyostosis (the thickness of the mandible in front of M3 measures 37 mm), a range consistent with the variation observed in *Megaloceros giganteus* samples from Ireland (28.1-41.5 mm; material stored in the Natural History Museum of London), the metacarpal Nr. 24.1.1938 (Friant 1957: pl. iv, fig. 6), and the metatarsal Nr. 16.3.1936 (Friant 1957: pl. iv, fig. 7). We affirm that the metapodial bones from Kent's Cavern correspond closely to metapodial measurements of the robust short-limbed form of the giant deer (Croitor *et al.* 2014). The radio-ulna Nr. 5.22, previously considered by Friant (1957: pl. iv, fig. 8) as evidence of complete fusion of the radius and ulna in the Kent's Cavern giant stag, belongs to a horse (Lister 1987b).

Nonetheless, Lister (1987b) confirmed that the osteological remains of the cave stag from Kent's Cavern surpass in size any living European red deer and are comparable in size to modern American and Siberian wapiti. Lister (1987b) also noted the stockier limb bones of the cervid remains from Kent's Cavern, described as "unusually short for their width". However, a definitive decision on the taxonomic classification of these postcranial bones requires larger samples of comparative material. Additionally, the variability of metapodials –bones that are well-represented in the paleontological record– among subspecies of red deer and wapiti remains unknown and necessitates future analytical study.

Ultimately, mitochondrial DNA analysis conducted on elaphine deer remains from Kent's Cavern revealed their affili-

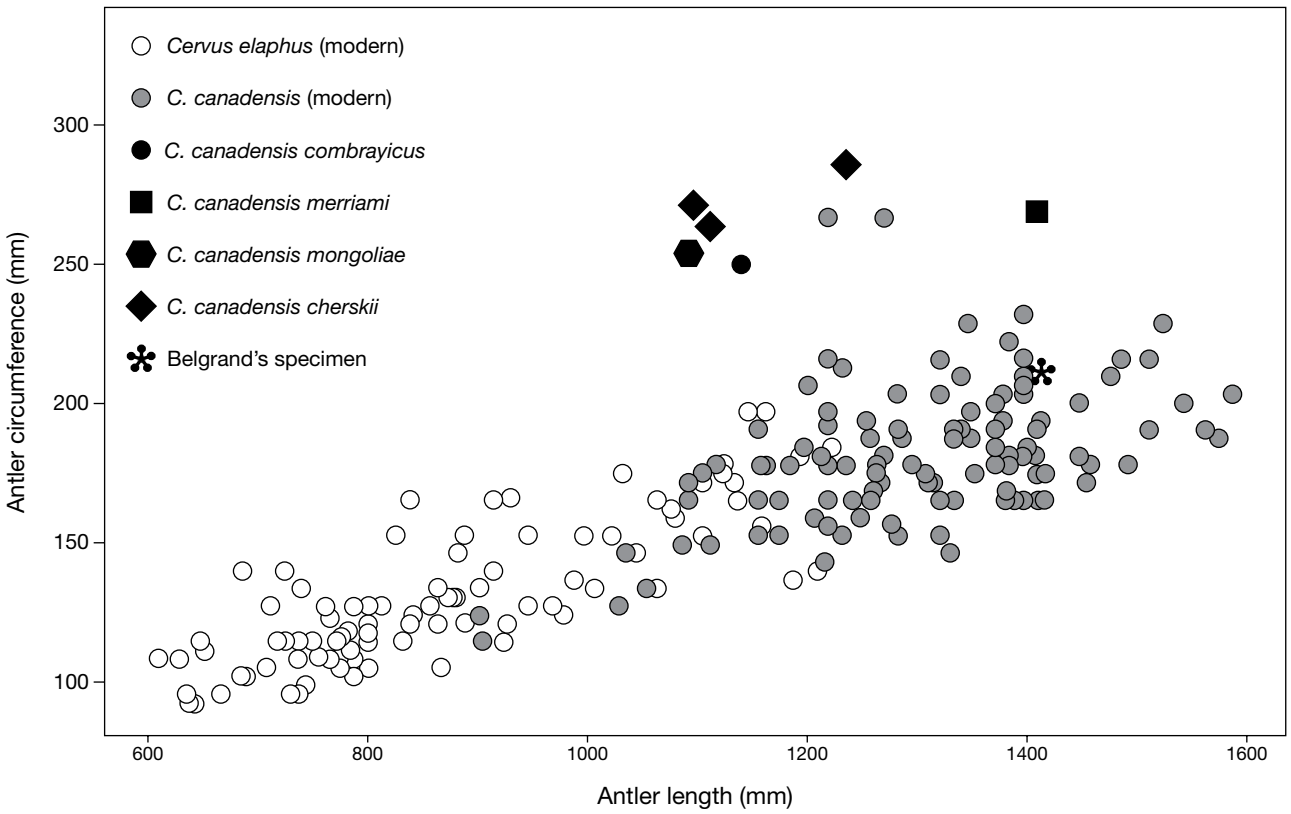

FIG. 6. — Bivariate plot illustrating the distribution of modern red deer (various subspecies), modern North American wapiti, and fossil Eurasian wapiti. Data for modern red deer *Cervus elaphus* Linnaeus, 1758 and wapiti *Cervus canadensis* Erxleben, 1777 are adapted from Ward (1892), while data for *Cervus canadensis cherskii* Boeskorov, 2005; *Cervus canadensis combrayicus* Croitor, 2020; *Cervus canadensis merriami* Nelson, 1902; and *Cervus canadensis mongoliae* Gaudry, 1872, are taken from original descriptions (Gaudry 1872; Nelson 1902; Boeskorov 2005; Croitor 2020a).

ation with the European red deer species *C. elaphus* (Meiri *et al.* 2013). Consequently, the inquiry into the presence of wapiti in the Kent's Cavern fauna remains unresolved. The absence of the most diagnostically significant distal portions of antlers in the European paleontological record constitutes the primary impediment to confirming the presence of wapiti *C. canadensis* in Western Eurasia (Friant 1957).

Prat & 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. 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 & Suire (1971), this size difference may have a taxonomical significance at the subspecies level.

Guadelli (1997) noted that the "larger elaphine" deer from Saint-Hippolyte (Puy-de-Dôme in Central France) bears resemblance to the large cervid form *C. elaphus* ssp. from Combe-Grenal. Furthermore, Guadelli (1997) delineated some dental morphology discrepancies between the "large elaphine" and "small elaphine" forms from Combe-Grenal. For instance, the "larger elaphine" deer exhibited relatively broader upper molars and a very frequent lingual groove in P2, indicating a stronger brachyodonty (a primitive morphological trait) and a more advanced degree of molarization of P2 (an advanced morphological trait). Guadelli (1997) also observed a more robust development of the entostyle and lingual cingulum in the molars of the "larger elaphine" deer, alongside a paraconid more frequently separated from the parastylid in P2, a more common and pronounced molarization of P4 (where the metaconid and paraconid are connected, closing the second dental valley), distinguishing the "large elaphine" deer from the "smaller" counterpart. Guadelli (1997) deemed these differences in dental morphology as taxonomically significant and proposed the species name *Cervus simpicidens* for the "smaller elaphine" deer from Combe-Grenal.

The assertion of the presence of two distinct "elaphine" deer in the Late Pleistocene of France found support from Croitor (2020a), who conducted a taxonomic reassessment of a large cervid skull with well-preserved antlers from Saint-Hippolyte, housed in the collection of the Natural History Museum of Clermont-Ferrand. The antlers of the specimen from Saint-Hippolyte exhibit a series of morphological characteristics, including the parasagittal orientation of the distal crown, flattening of the crown tines, and the absence of antler pearling in the distal part, suggesting that the fos-

sil deer in question belongs to *C. canadensis*. Furthermore, specific features such as the strongly divergent antler beams and the downward direction of the middle (trez) tine led to the description of the wapiti from Saint-Hippolyte as a new subspecies, *C. canadensis combrayicus* Croitor, 2020 (Croitor 2020a). The antlers of the wapiti from Saint-Hippolyte exhibit a higher degree of evolutionary specialization compared to those of *C. canadensis* specimens from the Late Paleolithic site of Climăuți II, Moldova (Croitor & Obada 2018). The wapiti antler from Climăuți II is virtually indistinguishable from those of *C. canadensis cherskii* Boeskorov, 2005, originating from the Upper Pleistocene of Eastern Siberia, and *C. canadensis mongoliae* (Gaudry, 1872) (= *C. canadensis fossilis* Zdansky, 1925), found in the Upper Pleistocene of Northeastern China.

The presence of *C. canadensis* in Europe during the cold phases of the Late Pleistocene is confirmed by paleogenetic studies revealing a close relationship between the modern Asian wapiti *C. canadensis sibiricus* / *songaricus* with the Late Pleistocene *C. canadensis cherskii* (Fig. 2C) and pre-Last Glacial Maximum specimens from Romania and Crimea (Stankovic *et al.* 2011; Meiri *et al.* 2018). Stankovic *et al.* (2011) consider the arrival of wapiti in Crimea as part of the invasion of cold-adapted forms into Eastern Europe at the end of the Würm II/Würm III Interstadial period (= MIS 3-MIS 2). The beam circumference and antler length of *C. canadensis cherskii*, *C. canadensis combrayicus*, and *C. canadensis mongoliae* place these fossil forms among the rare, exceptionally robust antlers observed in modern North American wapiti (Fig. 6). This remarkable robustness of antlers in both extinct wapiti forms and some modern individuals from North America may have diagnostic taxonomic significance. Unfortunately, the exact provenience of the specimens measured by Ward (1892) is not always available, making it impossible to provide a reliable interpretation of the exceptionally robust antlers from modern wapiti.

Summarizing all the diversity of fossil and sub-fossil specimens we identified as wapiti in Western Europe, we propose the following subspecies and forms:

– *C. canadensis spelaeus* (Owen, 1846) n. comb. (originally published as *Cervus* (*Strongyloceros*) *spelaeus* Owen, 1846), also known as the cave stag, from the Upper Pleistocene of England (MIS 3-MIS 2). Limited material makes it challenging to distinguish this wapiti subspecies. The primary characteristic available is the exceptionally large size of its antlers. The subspecies name *spelaeus* is retained mostly for historical reasons and lacks practical taxonomical or systematical significance;

– *C. canadensis combrayicus*, from the Late Pleistocene of France. Unlike modern wapitis, this subspecies exhibits adaptations to open landscapes: its antlers spread strongly sideways, with the middle (trez) tine pointing downward, possibly serving a function similar to the posterior tine in the giant deer *Megaloceros giganteus*. The crown part of the wapiti from Saint-Hippolyte appears relatively weak, possibly due to the young age of the animal (Fig. 2D);

– The isolated population of wapiti from the Holocene postglacial refugium in Sweden (Fig. 7A). This wapiti form is insufficiently described, as its remains are seemingly mixed with those of Holocene red deer *C. elaphus* (Ahlen 1965). The antlers of the remnant Holocene population of wapiti are palmated and resemble those of *C. canadensis palmidactyloceros* (De Stephano, 1911) n. comb.;

– *C. canadensis palmidactyloceros* (originally published as *C. elaphus palmidactyloceros* De Stefano, 1911), from the Upper Pleistocene and early Holocene of Northeastern Italy, the Apennine Mountains, and Swiss peat bogs (Abbazzi 1995 also referred there as *C. elaphus*). This well-distinguished subspecies of wapiti survived into the Holocene in the Alpine-Apennine refugium (Croitor 2020a). The distal part of its antlers became strongly flattened and even palmated, with the first crown tine bifurcated (Fig. 7B). To some extent, this extinct form of wapiti exhibits parallelism with the North American *C. canadensis merriami* in the development of antler palmation;

– *C. canadensis tyrrhenicus* (Azzaroli, 1961) n. comb. (originally published a *Cervus tyrrhenicus* Azzaroli, 1961), a subfossil dwarfed wapiti from the island of Capri, that we consider derived from *C. canadensis palmidactyloceros* (Croitor 2020a). Capri, intermittently connected to the Italian mainland, likely isolated the wapiti population after sea level rise in the Holocene. Evolutionary changes primarily affected the body size of *C. canadensis tyrrhenicus*, which did not exceed 100 kg. Its antlers lost the bez tine and the third crown tine but retained the bifurcated first crown tine and distal palmation (Fig. 7C).

Therefore, a thorough revision of some *Cervus* remains from the Late Pleistocene of Europe, especially those associated with cold faunas, is necessary. The occurrence of the cold-adapted *C. canadensis* in Europe during the Last Glacial Maximum explains the "paradoxical" presence of elaphine deer in the southern extension of permafrost areas in Eastern Europe, notably in the Late Paleolithic sites Rașcov 7 and Cosouți in Moldova (Sommer & Nadachowski 2006; Sommer *et al.* 2008). Banks *et al.* (2008) developed ecological niche models of red deer during the Last Glacial Maximum that do not support the hypothesis of the "East Carpathian Last Glacial Maximum refugium" of *C. elaphus*. The confusing reports of red deer presence in the Eastern Carpathian area stem from David (1980), where some cervid remains are misidentified or their stratigraphic positions erroneously indicated. For example, the presence of *C. elaphus* at the Late Paleolithic site of Rașcov 7 is based on a talus that actually belongs to *Ovibos moschatus* (Zimmermann, 1780) (Croitor 2020b).

The postglacial "red deer" remains studied by Drucker *et al.* (2011) from the Alpine environments of the French Jura, where it persisted in open landscapes and relatively cool conditions, most likely also belong to the remnant population of *C. canadensis* that survived during the early stages of the Holocene in the Alpine refugium. The remarkably elongated mandible's well-preserved horizontal ramus from an unknown deposit level of Soleilhac (Haute-Loire; central France), described as *Megaceros solilhacus* Azzaroli, 1979, most probably belongs to *C. canadensis*. One of such specimens

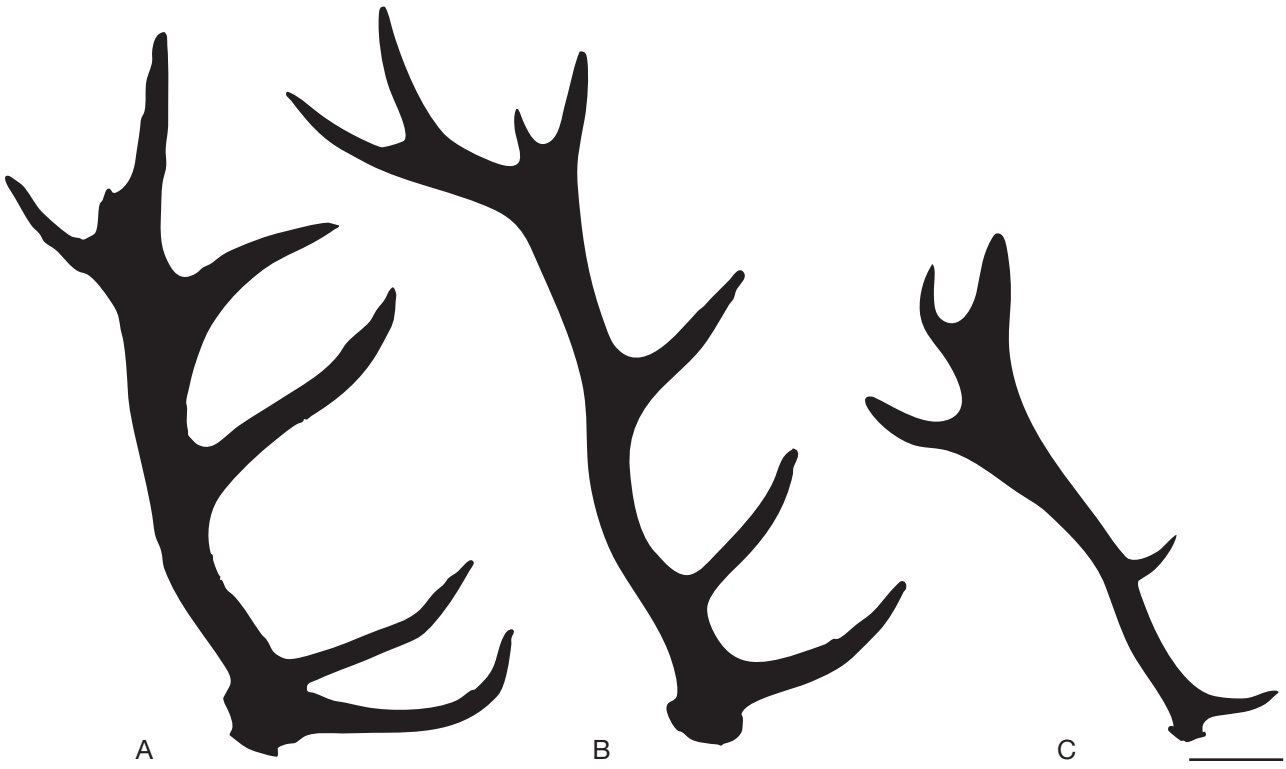

FIG. 7. — The Holocene forms of wapiti from Western Europe: **A**, *Cervus canadensis* Erxleben, 1777 from Balkakra, Sweden; **B**, *Cervus canadensis palmidactyloceros* (De Stephano, 1911) n. comb. (originally published a *Cervus elaphus palmidactyloceros* De Stefano, 1911) from Switzerland; **C**, *Cervus canadensis tyrrhenicus* (Azzaroli, 1961) n. comb. (originally published as *Cervus tyrrhenicus* Azzaroli, 1961) from the Island of Capri. Credits: A, adapted from Ahlen 1965; B, reconstruction based on specimens figured by De Stefano 1911; C, adapted from Azzaroli 1961. Scale bar: 10 cm.

is the mandible 2003-4-420-SOL from Soleilhac that was originally described as *Megaceros* (*Megaceroides*) *solilhacus* (= *Praemegaceros solilhacus*) by Azzaroli (1979: pl. 3, fig. 2). It is characterized by a very long diastema, which attains 82.6% of the lower tooth row length, approaching to the highest values of *C. elaphus*, and significantly longer than in species of the genus *Praemegaceros* (Croitor 2018). It is possible that the large-sized deer, *C. elaphus* sp., discovered in the upper levels of Combe-Grenal (layers 35 to 1; MIS 4; Guadelli 1997), is also a wapiti.

RED DEER *VERSUS* WAPITI

The morphological distinctions between wapiti and red deer pose a significant challenge. Comparative morphological studies of *C. elaphus* and *C. canadensis* have been limited, likely because these species were long regarded as groups of subspecies within the single species *C. elaphus*. Research efforts primarily focused on antler shape and linear cranial measurements, considered taxonomic criteria at the subspecies level (Heptner & Zalkin 1947). Consequently, available data on the morphological differences between these two species are scarce and incomplete, while size distinctions alone may be insufficient as a criterion. A comprehensive comparative study of cranial and dental morphology between wapiti and red deer has yet to be conducted.

TABLE 2. — Results of Student's t-test comparing antler beam circumference and antler length of various subspecies of *Cervus elaphus* Linnaeus, 1758 and *Cervus canadensis* Erxleben, 1777 from North America. Antler measurements are adapted from Ward (1892). Abbreviations: **CFR**, beam circumference above bez tine; **L**, total antler length.

Measurement	t-statistic	p-value
CFR	–13.545	1.07×10^{-30}
L	–21.005	3.42×10^{-54}

We found antler size, frequently cited by many authors as a key distinguishing feature between *C. elaphus* and *C. canadensis*, to be a statistically significant trait. Large datasets of hunting trophy antlers from red deer and wapiti, measured by Ward (1892), provide an excellent source for evaluating antler size (Table 1). The bivariate plot highlights a clear distinction in antler size between modern *C. elaphus* and *C. canadensis*, with fossil forms of wapiti exhibiting notably more robust antlers (Fig. 6). Our Student's t-test analysis revealed significant statistical differences in both antler length and beam circumference measured above the bez tine, with a p-value extremely close to 0 (Table 2). This suggests that antler beam circumference is a reliable character for species identification.

The regression model based on Ward's (1892) measurements of *C. elaphus* antlers demonstrate a good fit, with an R^2 value of 0.67, indicating that 67% of the variation in antler length (L) is explained by variation in antler circum-

ference (CFR) in the obtained regression model (Fig. 5). Additionally, Pearson's R of 0.82 suggests a strong positive correlation between antler circumference and antler length in the available data. The regression model based on available measurements of *C. canadensis* from North America is less accurate, with an R^2 value of 0.32 (Fig. 5), indicating that approximately 32 % of the variation in antler length can be explained by antler circumference in our model. Pearson's R of 0.57 suggests a moderate positive correlation between these two variables. When interpreting the results of this linear regression, it is important to consider that the dataset consists of hunter trophies (Ward 1892), meaning the sample is artificially selected, which may influence the observed relationship between antler parameters. Additionally, the sample likely represents a mixture of antlers from different subspecies, further contributing to variability in the data.

The equations of linear regression between antler beam robustness and antler length show that in modern wapiti, antler robustness increases more rapidly with increasing antler length (even after excluding a few exceptionally robust antlers as outliers that distorted the linear regression) than in red deer (Fig. 5).

Distinctive features in antler morphology are well-documented. Antlers of *C. canadensis* differ from those of *C. elaphus* by their generally less developed crown, typically consisting of three tines arranged in the parasagittal plane (Lydekker 1898; Heptner & Zalkin 1947; Geist 1998). Wapiti antler crowns rarely evolve additional tines, although they may become somewhat compressed from the sides and often exhibit palmations under optimal environmental conditions (Heptner & Zalkin 1947). For example, the type specimen of *C. canadensis merriami* from Arizona showcases such a variant with a flattened distal portion of the antler (Nelson 1902).

The position of the 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 the 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, evolving surface pearling only in the area of brow and bez tines (Stepanova & Argunov 2016).

We have limited knowledge regarding morphological distinctions in cranial morphology between red deer and wapiti. Heptner & Zalkin (1947) noted some general differences in cranial proportions of modern *C. canadensis* and *C. elaphus*: wapiti skulls are typically broader and more robust with a somewhat shorter facial part. The ratio of the face length, measured from the anterior part of the orbit rim to the tips of the premaxillary bones (prosthion), to the condylobasal length is generally below 60 % in wapiti, while in red deer, this ratio is typically above 60 %, especially in the largest red deer subspecies *C. elaphus maral*, although there is some overlap in the sample values (Heptner & Zalkin 1947).

From earlier descriptions of fossil wapiti or "large elaphoid" deer, we can identify the following dental morphological characters distinguishing the presumed fossil wapiti from European red deer: rugosity of enamel in cheek teeth, a strong entostyle in upper molars, relatively linguolabially broader upper molars, and a more frequent lingual groove in P2 (Pomel 1853; Gaudry 1876; Guadelli 1997).

Biometric analysis of skeletal remains is a methodologically reliable approach, as size differences between *C. elaphus* and *C. canadensis* seem to be statistically significant (Prat & Suire 1971; Guadelli 1997). Additionally, interesting insights may arise from differential statistical analysis of postcranial remains, as well as measurements of pearl-like upper canine beads used as adornments in Paleolithic societies. The upper canines of red deer and wapiti are also distinguishable by their size (Covalenco & Croitor 2022).

DISTRIBUTION OF RED DEER AND WAPITI IN EURASIA

The red deer and the wapiti, primarily distributed across the Holarctic region, exhibit fairly similar morphology. Both belong to the genus *Cervus*, which emerged in the early Quaternary around 2.6 million years ago. Their evolution and differentiation into two distinct species began in Asia. While the red deer experienced significant expansion in Europe, the wapiti, originating from eastern Asia, colonized North America. However, during the Pleistocene, the wapiti also migrated to Western Europe, where its fossilized remains are now identified.

The red deer, *C. elaphus*, thrives in deciduous and coniferous forest environments but also adapts to open spaces such as grasslands and is capable of colonizing high mountain valleys (Heptner & Zalkin 1947; Flerov 1952; Sokolov 1959). Its geographical distribution indicates dispersal from the Tarym area westward (Ludt *et al.* 2004). The earliest dispersal event occurred during the Early Pleistocene, marked by the presence of *Cervus nestii* in Georgia and Italy. By the early Middle Pleistocene, the paleontological record of Europe witnessed the dispersal of a larger species from the Glacial epoch, *C. elaphus*. Subspecies diversification and evolution of red deer during the Middle and Late Pleistocene are linked to Glacial refugia in the Iberian Peninsula, the Italian and Balkan Peninsulas, Anatolia, Transcaucasia, and Central Asia (Fig. 6). Thus, during glaciations, red deer acted as a typical warm-loving species, retracting its distribution to warm climate refugia. Glacial periods caused fragmentation of the red deer's distribution area, initiating evolutionary differences between subspecies (Ludt *et al.* 2004).

The evolutionary specialization of red deer subspecies increases from the east, where we find *C. elaphus bactrianus* with a simple terminal fork in the crown part of antlers and *C. elaphus maral* with a little branched crown and maintained spotting on the back in adult does, to

the West, where the nominotypical subspecies *C. elaphus elaphus* evolved the most advanced antlers with a richly branched antler crown and completely lost white spots on the back in adults. This pattern is a common phenomenon in mammalian biogeography, where we often observe the most evolved forms occurring at greater distances from the center of initial evolution.

The distribution dynamics of *C. canadensis* during the glacial periods diverged from those of *C. elaphus*. Geist (1998) characterizes wapitis as an eastern radiation of *Cervus*, migrating into dry, cold, continental regions and adapting to a grazing lifestyle in open landscapes. Modern wapiti subspecies encompass relatively primitive forms from mountainous areas of eastern Asia and more advanced forms from Siberia and North America. This distribution pattern reflects the relatively recent dispersals of wapiti from their initial area of distribution in eastern Asia to vast areas of northern Eurasia, coinciding with the onset of 40 000-year glacial cycles.

The significant dispersal of *C. canadensis* in Siberia began during the Kargin interglacial, when wapiti reached the Far North of Asia (Boeskorov 2005). By the last Glacial Period, the distribution of Eurasian wapiti extended from the Far East to Europe. The arrival of wapiti in Europe coincided with the retreat of red deer to southern glacial refugia. The survival of wapiti in postglacial Europe is also linked to refugia, albeit different ones where relatively cold ecological conditions persisted, allowing them to avoid direct competition with *C. elaphus*. These refugia have been located in the Alpine and Scandinavian regions. The relatively abundant subfossil remains of *C. canadensis palmidactyloceros* from Switzerland and Italy, along with articulated skeletons with antlers from southern Sweden, suggest that the Alpine altitudes and Scandinavia likely served as postglacial refugia for wapiti in Western Europe. *C. canadensis palmidactyloceros* from Switzerland, Italy, and possibly the French Alps, represents a relict population of wapiti that survived in Europe despite Holocene climate warming (Croitor 2020a).

Biogeographic, biological, and paleontological data suggest that *C. elaphus* and *C. canadensis* represent a typical example of vicarious species. The sharp geographical and genetic division between red deer and wapiti was established at least from pre-Last Glacial Maximum times (Meiri *et al.* 2018). The eastern border of the former species' range and the western border of the latter's shifted repeatedly eastwards and westwards with climate changes; thus, the dispersals of *C. canadensis* in Europe could have occurred several times (Stankovic *et al.* 2011; Meiri *et al.* 2018).

Wapiti, along with Late Pleistocene horses and steppe bison, became extinct across the vast North Eurasian region after the last glaciation. The distribution area of the modern north Asian wapiti, *C. canadensis sibiricus* (including the darker-colored *C. canadensis songaricus*, which is often regarded as a junior synonym of *sibiricus*), is limited to the mountain ranges spanning from Tian-Shan and Altai to Sayan and the southern Transbaikal Area (Heptner & Zalkin 1947; Flerov 1952; Danilkin 1999). From a biogeographic standpoint, this suggests that the modern Siberian wapiti should be viewed as a remnant of the successful Ice Age megafaunal species, which managed to survive the Holocene climate warming in the mountains of Central Asia acting as a glacial refugium. According to Stankovic *et al.* (2011), the modern Altai environmental conditions, where Asian wapiti survived, represent a recent analogue of the environment during the full-glacial period of Central Europe. This assumption was supported by Pavelková Řičánková *et al.* (2014), who noted a marked ecological similarity between recent eastern Altai-Sayan mammalian assemblages and Pleistocene faunas. The Last Glacial and recent eastern Altai-Sayan faunal assemblages are characterized by the co-occurrence of large herbivore and predator species associated with steppe, desert, and alpine biomes. According to Pavelková Řičánková *et al.* (2014), relic glacial fauna seems to persist up to the present in the Eastern part of the Altai-Sayan region, where, for instance, reindeer and saiga antelope still live in sympatry. Hence, *C. canadensis sibiricus* is another member of this relic fauna that has persisted from the glacial epoch to the present day.

CONCLUSIONS

The discourse in scientific literature regarding the presence of wapiti (*C. canadensis*) in Europe during the Late Pleistocene has a longstanding history dating back to the first half of the 19th century. Over time, the accumulation of information on biology, evolution, dispersal, and ecology of both red deer and wapiti has led to a fresh perspective on this issue and identified the research directions that are imperative to pursue.

Research in genomics and paleontology sheds light on the intricate taxonomy of both present-day and ancient cervids, along with their remarkable adaptive abilities. Recent paleontological updates have reshaped our understanding of the distribution patterns of both red deer and wapiti. During the Pleistocene epoch, according to our attribution of various specimens to the *C. canadensis* species instead of their original attribution to the *C. elaphus* species, wapiti expanded their range from Siberia to the far reaches of Western Europe, where they adapted to local conditions and diversified into various subspecies, including a smaller form that evolved in the condition of insular isolation. Scandinavia and the Alps acted as refuge areas at the transition from the Pleistocene to the Holocene, providing sanctuary for these species, which even reached as far as the Italian island of Capri. *C. elaphus* and *C. canadensis* occupy distinct ecological niches, underscoring the importance of accurately identifying fossil remains from prehistoric sites. This determination can offer insights into environmental conditions and hunting strategies, considering the differences in body size and ecological needs between the two species. Recent discoveries of fossil wapiti in Western Europe highlight the necessity of conducting comparative studies to distinguish diagnostic features between red deer and wapiti. Despite advancements, the natural history of the genus *Cervus* remains inadequately explored and warrants further attention from researchers.

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