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Roman Croitor

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ROMAN CROITOR

**PLIO-PLEISTOCENE DEER OF WESTERN
PALEARCTIC:
Taxonomy, Systematics, Phylogeny**



Institute of Zoology of the Academy of Sciences of Moldova

Chișinău 2018

Roman Croitor

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Taxonomy, Systematics, Phylogeny**

Under the scientific redaction of
Ion Toderaş

Institute of Zoology of the Academy of Sciences of Moldova

Chişinău 2018

On the cover: the side view of the antlered skull of *Eucladoceros ctenoides falconeri* (Dawkins, 1868) from Sénèze (the holotype of *Cervus darestei* Depéret, 1931) stored in the Paleontological Museum of the University of Lyon, France (the collection number 16128).

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INTRODUCTION

Systematics and phylogeny of the Family Cervidae: the state of the art. The deer represent one of the most successful and rich in species group of large-sized herbivores in the modern fauna of Eurasia and Americas. In the geological past, the family Cervidae was represented by a significantly broader variety of evolutionary and ecological forms, which exemplify the numerous biogeographic and evolutionary cases of parallelism and convergence, the broad phylogenetical radiation in the newly colonized mainland, the evolution in conditions of insular isolation, or the endemism forms in continental biogeographic refugia (Lydekker 1898; Azzaroli 1961; Gliozzi & Malatesta 1982; Lister 1987; Vislobokova 1990; Geist 1998; Croitor 2006b, 2014; Croitor et al. 2006).

The earliest publications from 17th and 18th centuries describing the fossil deer represented rather reports on natural curiosities (for example, Knowlton 1746; Barker 1785), therefore the descriptions of the fossil remains were not sufficiently exact and accurate, however, they served as a scientific basis for the subsequent synthetic systematical studies of the fossil deer (Cuvier 1823). According to the paradigm of the systematical classification of the animal world of that time, all cervid species were placed in the genus *Cervus* (Linnaeus 1766). Even much later, when new genera and subgenera of the modern and fossil deer were proposed, the genus *Cervus* continued to be used as a temporary taxonomical container for poorly known species with an unclear systematical position. This broadly accepted arbitrary taxonomical solution was applied for many decades and is mostly caused by the specific character of paleontological domain, as the fossil animal forms are often represented by poor and fragmentary remains that need to be described and classified.

Despite of the great number of important paleontological discoveries made since the 19th century, our knowledge on fossil deer evolution advanced in a lesser degree. Vague, incomplete or imperfect original descriptions of old species cause taxonomical confusions complicated by multiple synonymies and lack of methodologically uniform criteria in taxonomy and systematics of the fossil deer. Many of fossil cervid forms remain little known, poorly understood, or misinterpreted. Despite of the great variety of proposed cervid classification schemes and phylogenetic models, the visible progress is impeded by the incomplete and confused taxonomical data.

The first attempt to build a founded classification of the family Cervidae belongs to Brooke (1878), who described two types of reduction of the second and fifth metacarpals in cervids, represented by their proximal (plesiometarcarpal condition) or distal (telemetarcarpal condition) remnants. According to the reduction type of lateral metacarpals, Brooke (1878) established two cervid groups: the “Plesiometarcarpi” group that includes the Old World deer except for *Capreolus* and *Hydropotes*, and the “Telemetarcarpi” group that includes mostly the New World deer (except for *Cervus canadensis*), the Old World genera *Capreolus* and *Hydropotes*, as well as the circumpolar and circumboreal genera *Rangifer* and *Alces*. Among “Plesiometarcarpi”, the modern

genus *Muntiacus* represents the most advanced morphological condition expressed in a complete reduction of lateral (second and fifth) digits (Brooke 1878). Brooke (1878) indicates also a certain correlation between the telemetacarpal morphological condition and the complete dividing of nasal cavities by vertical plate of vomer in combination with some other morphological characters, therefore giving a zoogeographic, systematic, and phylogenetic importance to the observed characters. Brooke (1878) also suggests that the bone septum completely dividing the nasal choanae in American deer is a primitive character shared with less specialized artiodactyls like *Hippopotamus*, *Sus* and *Tragulus*. Brooke's (1878) terms "Plesiometacarpi" and "Telemetacarpi" are not available according to the rules of ICZN, but they were considered later as equivalents of cervid subfamilies Cervinae Goldfus 1820 and Capreolinae Brookes, 1828 (= Odocoileinae Pocock 1923) correspondingly (Frick 1937; Grubb 2000; Gilbert et al. 2006).

Lydekker (1898) ignored the taxonomical significance of the type of lateral metacarpal reduction in cervids and proposed a simplified classification of the family Cervidae, which contained only two subfamilies: the subfamily Cervinae ("the true deer") with all modern genera of plesiometacarpal and telemetacarpal deer, as well as the extinct genera *Dremotherium*, *Dicrocerus*, and *Anoglochis*, and the subfamily Moschinae ("the aberrant deer") with the single genus *Moschus*. Lydekker (1898), however, makes a reservation with respect to his cervid classification; he admits that the subfamilies Cervinae and Moschinae can be regarded as families, while cervid genera may be grouped in subfamilies, without, however, specifying which subfamilies.

Simpson (1945) proposed the first important systematical generalization of cervids. He recognized six main branches, or subfamilies, in the composition of family Cervidae: Palaeomerycinae Mathew, 1904; Moschinae Zittel, 1893; Dromomerycinae Frick, 1937; Muntiacinae Pocock, 1923 (including Simpson's new tribe Dicrocerini with the type genus *Dicrocerus*; the genera names *Heteroprox* Stehlin, 1928, and *Euprox* Stehlin, 1928 were included in the synonymy of *Dicrocerus*); Cervinae Baird 1857 (including Pliocervinae Khomenko, 1913); and Odocoileinae Pocock, 1923 (including Capreolidae Brookes, 1828; Alcinae Jerdon, 1874; Rangiferinae Pocock, 1923; and Hydropotinae Trouessard, 1878). According to Simpson (1945: p. 267), the phyletic relationship between *Dicrocerus* and *Muntiacus* is not certain, however those genera represent a similar evolutionary stage and it is at worst a convenient morphological grouping of these and other similar cervids in the subfamily Muntiacinae.

Flerov (1952) divided the cervid family into five subfamilies, disregarding the plesiometacarpal and telemetacarpal division: Palaeomerycinae Matthew, 1904 (including *Dremotherium* and *Palaeomeryx*); Dromomerycinae Frick, 1937; Cervulinae Sclater, 1870 (= Muntiacinae); Cervinae Baird, 1857 (including *Pliocervus*, *Cervavitus*, *Procapreolus*, *Capreolus*, and *Alces*); Neocervinae Crette, 1922 (= Capreolinae Brookes, 1828, = Odocoileinae Pocock, 1923); and Hydropotinae Trouessard, 1898. According to Flerov (1952), the Late Miocene *Cervavitus* represents a transitional link

between the muntjac-like *Dicrocerus* and the modern *Cervus* and other closely related Cervinae forms, while the arbitrary group of the “American deer” resulted from the local evolutionary process of Miocene *Blastomeryx*. Flerov (1952) proposed also the hypothesized phylogenetic relationships of modern cervids with the fossil forms.

Azzaroli (1953) proposed a similar classification for the living deer, which are divided into seven subfamilies: Cervinae Baird, 1857; Muntiacinae Pocock, 1923; Capreolinae Capreolinae Brookes, 1828; Odocoileinae Pocock, 1923; Rangiferinae Pocock, 1923; Alcinae Jerdon, 1874; and Hydropotinae Trouessard, 1898.

Two important family group taxa were created for the fossil deer forms that have no analogues in the modern animal world: the subfamily Pliocervinae Khomenko, 1913 and the tribe Megacerini Viret, 1961.

In 1913, Khomenko established the subfamily Pliocervinae in order to designate the transitional evolutionary stage between the primitive muntiacines and the advanced cervines of the modern type. Khomenko's Pliocervinae contained new genera and species *Cervocerus novorossiae*, *Cervavitus tarakliensis*, and *Damacerus bessarabiae*, as well as *Cervus matheroni* Gervais, *Dremotherium pentelici* Gaudry, and *Cervavitus speciosus* Schlosser (Khomenko 1913). However, Pliocervinae Khomenko is not based on any genus-group name and therefore is not available according to Article 29 of the ICZN. The proposed by Symeonidis (1974) subfamily Pliocervinae, which can be taken to be based on *Pliocervus* Hilzheimer, 1922 (*C. matheroni* is the type species), and therefore this is an available family group name (Grubb 2000).

The tribe Megacerini Viret, 1961 originally based on a single species *Megaloceros giganteus* Blumenbach (Viret 1961), became later a taxonomic unit used as a receptacle for large-sized Old World fossil cervids with obscure phylogenetic relationships and their assumed small-sized relatives. This taxonomic group was accepted by some researchers (Czyżewska 1968; Lister 1987; Vislobokova 1990, 2009; Di Stefano & Petronio 2002). Vislobokova (1990, 2009, 2012, 2013) regarded the giant deer as a well-outlined phylogenetic group of cervines and included in the tribe Megacerini up to 11 genera from Eurasia and Mediterranean islands with the geological range from Late Miocene to Early Holocene. According to Grubb (2000), the tribe Megacerini Viret, 1961 is a junior synonym of Megalocerotinae Brookes, 1828.

Czyżewska (1968) summarized the classifications published by the previous authors (Khomenko 1913, Simpson 1945, Flerov 1952, Azzaroli 1953, Viret 1961) and proposed to distinguish the following tribes within the subfamily Cervinae Baird 1857: Pliocervini Khomenko, 1913 with the genus *Cervavitus* Khomenko, while *Pliocervus* Hilzheimer, 1922 is regarded as *incertae sedis*; Capreolini Simpson, 1945, Cervini Weber, 1928; Alcini Simpson, 1945; and Megacerini Viret, 1961. According to Czyżewska (1968), the genus *Euprox* (subfamily Cervulinae, = Muntiacinae) is ancestral for two sister lineages: Capreolini and Pliocervini+Cervini. Czyżewska (1968) regarded Asian “Pliocervini” as probable ancestors of *Axis* and *Cervus*. Petronio et al. (2007) attributed the authorship of the tribe Pliocervini to Czyżewska, 1968, but this is not the case.

Groves & Grubb (1987) proposed the division of modern deer into three subfamilies (Hydropotinae, Odocoileinae, and Cervinae). Later, Groves & Grubb (1990) included muntjacs in their own family Muntiacidae. According to the emended classification Grubb (2000), the family Cervidae includes the following subfamilies: Hydropotinae Troussard, 1898; Lagomerycinae Pilgrim, 1941 (with tribes Lagomericini Pilgrim, 1941 and Dicrocerini Simpson, 1945); Pliocervinae Symeonidis, 1974 (with genera *Cervavitus* and *Pliocervus*); Capreolinae Brookes, 1828 (with tribes Capreolini Brookes, 1828; Odocoileini Pocock, 1923; Alceini Brookes, 1828; Rangiferini Brookes, 1828); and Cervinae Goldfuss, 1820 (with tribes Muntiacini Knotterus-Meyer, 1907 and Cervini Goldfuss, 1820). Grubb (2000) included in the tribe Muntiacini only modern muntjacs from South-Eastern Asia and the extinct Chinese genus *Eostyloceros*. Grubb (2000) was the first who confirmed the polyphyletic character of the arbitrary group of “primitive” muntjac-like cervids and treated them as members of two different subfamilies: Lagomerycinae and Cervinae.

The systematical work of Bouvrain et al. (1989) is remarkable for the complex methodological approach that involved the karyotype, morphological, and biochemical data. The obtained by Bouvrain et al. (1989) results supported the monophyly of the subfamilies Cervinae and Odocoileinae. The subfamily Odocoileinae, according to Bouvrain et al. (1989), includes also *Capreolus*, *Alces*, and *Rangifer*. The phyletic position of *Hydropotes* is regarded as uncertain, but closely related to Odocoileinae.

Vislobokova (1990) accepted Simpson’s (1945) classification with some modifications and maintained the separation of plesiometacarpal and telemetacarpal cervids. According to Vislobokova (1990), the family Cervidae includes five modern subfamilies: Muntiacinae Pocock, 1923 (with tribes Dicrocerini Simpson, 1945 and Muntiacini Pocock, 1923); Cervinae Baird, 1857 (with tribes Pliocervini Khomenko 1913, Cervini Gray, 1821, and Megacerini Viret, 1961); Odocoileinae; Alcinae; Hydropotinae; and three extinct subfamilies: Dremotheriinae Ginsburg et Heintz, 1966; Dromomerycinae Frick, 1937; and Lagomerycinae Pilgrim, 1941. Vislobokova (1990) suggests that the divergence of modern cervid subfamilies took place during the Early and Middle Miocene. According to Vislobokova (1990), the modern genus *Muntiacus*, together with the extinct *Eostyloceros*, *Paracervulus* and *Metacervulus*, take their origin from the Early and Middle Miocene Eurasian *Euprox*. The forerunner of Cervinae is also sought among the Middle Miocene Muntiacinae (genus *Dicrocerus*). Vislobokova (1990) included the tribe Pliocervini Khomenko, 1913 with genera *Cervavitus* Khomenko, 1913 and *Pliocervus* Hilzheimer, 1922 in the subfamily Cervinae, stipulating, however, the uncertain systematic position of *Pliocervus*.

Di Stefano & Petronio (2002) rejected the taxonomical importance of the type of reduction of the lateral metacarpal bones with reference to the earlier study of Lister & Chapman (1988) on variability of the lateral metacarpals in some modern deer. Indeed, Lister & Chapman (1988) reported a broad individual variation of the atavistic vestiges of lateral metacarpals caused by genetic bottleneck and inbreeding

in British populations of the fallow deer. Lister & Chapman (1988) cautiously regarded the parallel development of plesiometacarpality in Muntiacinae and Cervinae as a possibility, however, they did not put in question the taxonomic and phylogenetic significance of the plesiometacarpal and telemetacarpal morphological conditions for the cervid taxonomy and systematics. Di Stefano & Petronio (2002) lumped together all antlered telemetacarpal and plesiometacarpal deer with the large complicated antlers in the subfamily Cervinae with six modern tribes (Neocervini Kalandadze & Rautian, 1992 [actually, the authorship belongs to Carrette, 1922]); Odocoileini Pocock, 1923; Rangiferini Simpson, 1945; Alcini Simpson, 1945; Capreolini Brookes, 1828; Cervini Goldfuss, 1820) and two extinct tribes (Pliocervini Symeonidis, 1974 and Megacerini Viret, 1961).

The proposed here very brief survey of various views on the systematics and classification of the family Cervidae reveals the lack of consensus in the classification of fossil and modern cervids. The disagreements on cervid systematics and phylogeny were caused by multiple unresolved questions, such as the poorly understood evolutionary specializations within the phylogenetic lineages, the objectively incomplete fossil record of cervids, and superficial, inadequate, or inaccurate initial descriptions of fossil cervid forms.

The misunderstood or poorly understood evolutionary significance of specific morphological characters provoked the controversial and long lasting debates on phylogenetic positions of some genera and phyletic lineages. This is the case of the telemetacarpal genera *Capreolus*, *Hydropotes* and *Alces* with *Cervalces*. The antlerless *Hydropotes inermis* for a long time was considered as the most primitive cervid that represents the initial evolutionary stage of the family Cervidae and was isolated in the subfamily Hydropotinae opposed to all antlered deer (Flerov 1952; Azzaroli 1953; Groves & Grubb 1987; Vislobokova 1990; Danilkin 1999; Grubb 2000; Di Stefano & Petronio 2002).

Elks (the genera *Alces* and *Cervalces*) represent another problematic isolated cervid group with unresolved phylogenetic relationships. The extreme morphological specialization of elk antlers and skulls do not show a clear affinity with any of the cervid groups and partly due to this unresolved phylogenetic problem all elks were placed in the separate subfamily Alcinae (Azzaroli 1953; Vislobokova 1990; Boeskorov 2001). Flerov (1952) and Sokolov (1959) included *Alces* in the subfamily Cervinae. Bouvrain et al. (1989) placed *Alces* within the subfamily Odocoileinae. According to Geist (1998), the elk (or moose) branched off from other New World deer in the late Tertiary.

Azzaroli (1953) included *Capreolus* in its own subfamily Capreolinae and suggested a more or less close relationship between Capreolinae and Alcinae based on the affinity in the dental morphology. Flerov (1952) regarded *Capreolus* as a primitive cervid close to muntjac-like evolutionary stage and included this genus in the subfamily Cervinae. Flerov's (1952) point of view was followed by Sokolov (1959), Czyzewska (1968), and Di Stefano & Petronio (2002). More often roe deer (together with Mio-Pliocene

Procapreolus) is grouped with the American deer in the subfamily Capreolinae (=Odocoileinae) (Simpson 1945; Korotkevich 1988; Bouvrain et al. 1989; Vislobokova 1990; Vislobokova & Kalmykov 1994; Danilkin 1999; Grubb 2000).

The phylogenetic relationships and origin of the Eurasian plesiometacarpal deer (cervines) are less debated, but not convincingly demonstrated and still require a critical reconsideration. Traditionally, the muntjacs and the large plesiometacarpal deer with complicate antlers are separated at the subfamily level or even are placed in different families (Khomenko 1913; Simpson 1945; Flerov 1952; Azzaroli 1953; Korotkevich 1988; Grooves & Grubb 1990; Vislobokova 1990; Di Stefano & Petronio 2002). The inclusion of all plesiometacarpal deer in the single subfamily Cervinae (Groves & Grubb 1987) is a less supported point of view. The Late Miocene holometacarpal *Cervavitus novorossiae* is often regarded as the most primitive member of the Cervinae. This viewpoint is based on the old repeatedly quoted in the Russian literature hypothesis of Khomenko (1913) on the mixture of muntiacine and cervine characters in the cranial morphology of *Cervavitus*. The phylogenetic relationships among the fossil cervines in most cases remained unclear, or poorly supported. Often the phylogenetic interpretations of fossil cervid forms are based on a limited set of arbitrarily selected or available characters: antler and cranial morphology (Vislobokova 1990), antler shape (Azzaroli & Mazza 1992; Di Stefano & Petronio 2002), postcranial morphology (Pfeiffer 1999), or general eco-morphology (Flerov 1952). Of course, a reference to a fossil cervid species or genus as a “transitional” or “ancestral” form should be regarded in a larger sense as an indication of a certain evolutionary stage represented by that fossil form, as, for instance, the case of *Cervavitus novorossiae* proposed as a transitional form between the primitive muntjac-like deer and the „true deer” of the subfamily Cervinae.

The main taxonomical difficulty of the subfamily Cervinae is caused by the relative uniformity of cranio-dental morphology that caused a difficulty in distinguishing genera. Some authors (Flerov 1952) accept a very broad understanding of the genus *Cervus*, that includes the rusa deer, the axis deer, as well as the fallow deer. The opposite viewpoint is proposed by Pocock (1942, 1943a, b, c) who regognized the valid status for the genera *Cervus*, *Axis*, *Hyelaphus*, *Panolia*, *Rucervus*, *Przewalskium* within Cervinae.

The relationship between the modern cervid taxa and the fossil forms remained little studied and in most cases speculative. Actually, there is a deep taxonomical gap between modern and fossil deer despite of some attempts to trace a connection between fossil cervid forms and the modern genera (Flerov 1952; Di Stefano & Petronio 2002).

Antlers traditionally are used as the main source of the diagnostic morphological characters used in descriptions of fossil deer species and genera and, consequently, are involved in the phylogenetic studies. This is explained by the fact that antlers represent the most specific, morphologically well-defined, and expressive fossil cervid remains that are relatively abundant in the fossil record. The antler shape is closely related to the social behavior and reproduction of deer (Geist 1998), therefore antlers may be regarded as a quite safe source of information for species description,

despite of the well-known individual, geographical, ontogenetic, and pathological variability of antler morphology (Heintz 1970). Unlike the paleontological taxonomy, the mammalian (including Cervidae) neontological taxonomy is essentially based on the skull morphology, therefore the fossil and the modern cervid taxa of the species and genus level are often based on different morphological criteria, which are difficult to correlate and result the methodological incompatibility between paleontological and neontological taxonomic data. Thereby, as Simpson (1945) rightly pointed out, the classification of living cervids is relatively easy to arrange; nonetheless, despite of the great abundance of fossil forms, they shed little light on the phylogenetic interrelationships of the modern deer.

Recent molecular phylogeny studies of modern deer. During the last two decades, the analysis of mitochondrial and nuclear DNA sequences made a great advance in the understanding of the phylogeny of modern cervids. The results on cervid molecular phylogeny is a new and very helpful tool to understand and interpret of the fossil deer record. According to the molecular analysis, the divergence between plesiometacarpal and telemetacarpal deer is an important basal event in the modern cervid phylogeny that took place in the Late Miocene (8.7-10.4 Ma according to Douzery & Randy 1997; 7.8-7.9 Ma according to Gilbert et al. 2006; or 10.7-11.5 Ma according to Hassanin et al. 2012). A little expected close phylogenetic relationship between *Capreolus* and *Hydropotes* was revealed; all Old World telemetacarpal cervids (*Alces*, *Capreolus*, *Rangifer*, and *Hydropotes*) together with the New Old deer form a monophyletic clade of telemetacarpal cervids (Douzery & Randy 1997; Randi et al. 1998; Pitra et al. 2004; Gilbert et al. 2006). The clade Capreolini-Hydropotini-Alcini emerged during the Middle Miocene between 15.6 and 16.8 Ma ago, and remains quite distant from the New World tribes of Capreolinae (Odocoileini and Rangiferini) (Randi et al. 1998). Hassanin et al. (2012) report a more recent dichotomy of the Eurasian (including *Alces*) and American Capreolinae (8.7-9.6 Ma).

The strong support for the close phylogenetic association between the Cervinae and the Muntiacinae (Miyamoto et al. 1990; Pitra et al. 2004; Gilbert et al. 2006) apparently was less expected since the modern muntjacs together with the extinct muntjac-like primitive cervids traditionally were placed in the subfamily Muntiacinae at the base of the cervid phylogenetic tree (Simpson 1945; Flerov 1952; Vislobokova 1990). However, the close phylogenetic association between modern muntjacs and cervines (subfamily Cervinae) agrees with most of the available morphological and biochemical data (Brooke 1878; Bouvrain et al. 1989). Therefore, the plesiometacarpal condition among the modern cervids apparently evolved only once through the reduction of lateral metacarpals. The new data on cervid phylogeny confirm the taxonomical importance of the type of reduction of lateral metacarpals and supports the natural character of modern plesiometacarpal cervid group (Randi et al. 1998).

The morphological analysis of the bony labyrinth carried out by Mennecart et al. (2017) brings very interesting results that open vast prospective in the phylogenetic

study of the fossil cervids. Mennecart et al. (2017) confirmed the monophyly of the Old World telemetacarpal deer (subfamily Capreolinae) and identified *Euprox furcatus* as a member of the subfamily Cervinae that diverged very early from the main Cervine phylogenetic branch, while modern *Muntiacus* belongs to the zoogeographically more restricted South-East Asian radiation together with large cervines. The methodology developed and used by Mennecart et al. (2017) is of great interest, since it permits to involve both modern and fossil forms in the phylogenetic studies.

The radiation of the advanced plesiometacarpal Old World deer appear to be an older event that occurred roughly from the Miocene/Pliocene boundary (3.3- 7.1 Ma) to the Early Pleistocene (0.4-2.5 Ma; the radiation of subspecies within *Cervus elaphus*) (Douzery & Randy 1997). Pitra et al. (2004) revealed the early divergence of *Axis axis*, *Rucervus schomburgki*, and *Rucervus duvaucelli* from the main phylogenetic stock of Cervinae. The white-lipped deer *Przewalskium albirostris* is a sister species to a wapiti/shou/sika clade of the genus *Cervus* (Pitra et al. 2004). The divergence of *Dama*, the only modern cervid genus that is not known from South-East Asia, from *Cervus* and allied cervines from South-Eastern Asia took place quite early, during the Early Pliocene (Pitra et al. 2004), or around 3.0 Ma (Gilbert et al. 2006). The results of the molecular phylogeny analysis also revealed the unexpected importance of the hybridization in the evolution and origin of modern cervid species. At list two evolutionary events of this type are recorded among the modern cervids: the non-monophyletic origin of red deer/wapiti group that before was regarded as a single species *Cervus elaphus* (Polziehn & Strobeck 1998; Kuwayama & Ozawa 2000; Ludt et al. 2004) and the origin of the puzzling species *Elaphurus davidianus*. The genus *Elaphurus* apparently resulted from hybridization ♀*Panolia eldi* (or a very close form) × ♂*Cervus canadensis* and therefore is close to the phylogenetic stock of *Cervus* and related forms (Meijaard & Groves 2004; Pitra et al. 2004).

In the light of new data, the genus *Muntiacus*, which traditionally exemplified a primitive forerunner of all modern deer, actually is the quite specialized taxon (the plesiometacarpal condition in *Muntiacus* attained the highest evolutionary degree) of the modern evolutionary radiation of the subfamily Cervinae. Certainly, *Muntiacus* still reminds the “adaptive constellation” (*vide* Geist 1998) that reminds the hypothesized ancestral type of Cervidae was a small-sized, cryptic, holometacarpal forest inhabitant with large tusks, long pedicles and small simple antlers (Flerov 1952; Czyżewska 1968; Janis & Scott 1987; Vislobokova 1990; Geist 1998). The enlarged upper canines are well developed in the majority of Miocene Cervidae, including the earliest representatives of Cervinae (apparently, this is the case of “*Cervavitus*” from the Late Tertiary of China) and Capreolinae (*Cervavitus*, *Pliocervus*, and *Procapreolus* from Western Eurasia) (Vislobokova 1990; Gentry et al. 1999).

Groves & Grubb (2011) updated their previous views on cervid nomenclature (Groves & Grubb 1987) and proposed to divide the modern cervids into subfamilies Capreolinae Brookes, 1828 and Cervinae Goldfuss, 1820. The subfamily Capreolinae, according to Groves & Grubb (1987), includes the tribe Rangiferini Brookes, 1828

with the circumpolar genus *Rangifer* and all American telemetacarpal genera, the tribe *Capreolini* Brookes, 1828 with the genera *Capreolus* and *Hydropotes*, and the monotypic tribe Alceini Brookes, 1828. The subfamily Cervinae includes the tribe *Muntiacini* Knottnerus-Meyer, 1907 with modern genera *Muntiacus* and *Elaphodus*, the tribe Cervini Goldfuss, 1820 with genera *Cervus*, *Axis*, *Dama*, *Rucervus*, *Panolia*, and *Elaphurus* (Groves & Grubb 2011). This classification of modern cervids is accepted in the present study.

The results of cervid molecular phylogeny studies adjust our knowledge on the systematics of the modern deer and permit to rethink the taxonomical value of such characters of modern cervid forms, as the antler complexity and other exosomatic characteristics, which seem to depend on the climatic-related lifestyle factors (Groves 2005). The new data on cervid evolution also offer a good opportunity for the revision of taxonomical criteria used to designate the fossil species and to elaborate a new look upon the phylogenetical and evolutionary relationships among fossil and modern cervid forms and clades.

In the present work, I propose a synopsis of systematical and taxonomical revision of cervid genera, species, and yet undescribed forms from the Pliocene and Pleistocene of the Western Palearctic with an attempt to reveal their possible phylogenetic relationships. Of course, this study cannot answer all questions on systematics and evolution of deer from the Western Palearctic, first of all, because the paleontological record still remains incomplete, while some important paleontological collections, unfortunately, are not included in the present study. Due to the specific character of cervid biogeography, almost all Plio-Pleistocene cervid forms from the Western Palearctic, with few exceptions, represent the terminal evolutionary forms of their lineages that evolved outside the area considered in the study. Therefore, the phylogenetic relationships of cervid lineages from Plio-Pleistocene of Western Palearctic on a larger scale remain hypothesized and require further studies.

MATERIAL STUDIED

The proposed study is based on the systematical revision of the Plio-Pleistocene deer of the Western Palearctic (Europe, the Near East, and North Africa), including the revision of the type material (61 type specimens, including holotypes, neotypes, syntypes, lectotypes, paralectotypes, and paratypes), the taxonomical study, and the study of additional dental and, when it is possible, cranial material in order to approach the systematic description of fossil species to the methodological standards applied in description of modern species. The studied fossil material is stored in the following collections:

- the Museum of Geology and Paleontology of the University of Florence, Italy (MGUF);
- the Geological School of the University of Thessaloniki, Greece (GSUT);
- the Natural History Museum of London, the United Kingdom (NHML);
- the musée national de Préhistoire, les Eyzies-de-Tayac, France (MNP);
- the Muséum national d'Histoire naturelle, Paris, France (MNHN);
- the Paleontological Museum of the University of Lyon, France (PMUL);
- the Institute of Zoology of the University of Wrocław, Poland (IZW);
- the Paleontological Institute, Moscow, Russia (PIN);
- the National Museum of Natural History, Kiev, Ukraine (MNHK);
- the Institute of Zoology, Chişinău, Moldova (IZC);
- the Natural History Museum "Grigore Antipa", Bucharest, Romania (NHMB);
- the Institute of Speleology "Emil Racoviţă", Bucharest, Romania (ISB);
- the Regional Museum "Oltenia" Craiova, Romania (RMO);
- the State Museum of Natural History of Stuttgart, Germany (SMNH);
- the Museum of Paleontology of the Department of Earth Sciences, the University of Rome "Sapienza", Italy (MPS);
- the Regional Museum of Prehistory of Menton, France (RMPM);
- the Rostov-upon-Don State University, Russia (RSU);
- the Musée Crozatier au Puy-en-Velay, France (MCP).

The osteological material of modern deer stored in the MGUF, MNHN, NHML, and IZUW is also involved in the study.

RESEARCH METHODS

The main methodological difficulty of the present study is the difference in the approach of the cervid species description used by paleontologists and neontologists. The cranial morphology is an important part of diagnoses of modern cervid species and, in particular, genera (Pocock 1942, 1943a, b, c; Flerov 1952; Sokolov 1959; Danilkin 1999). However, the definitions of the majority of fossil deer taxa are based mostly on antler morphology (Croizet & Jobert 1828; Dawkins 1872, 1878, 1887; Lydekker 1898; Schlosser 1924; Azzaroli 1953, 1992; Kahlke 1956, 1963, 1965; Heintz 1970; Korotkevich 1970; Pfeiffer 1999; Di Stefano & Petronio 2002); in some cases, species diagnoses are based on dental remains (Lydekker 1890; Heintz & Poplin 1980) or postcranial bones (Kahlke 1997). This methodological discrepancy is caused by the relative rarity of well-preserved skulls in the fossil record and makes the matching of fossil cervid forms with modern species difficult, if not impossible. Therefore, a special attention in this study is focused upon cranial morphology in the cases where the cranial material is available.

Measurements. The measurements of skulls, dentition, antlers, and postcranial bones are taken according to the well-known methodology described by Heintz (1970), Korotkevich, (1970), von den Driesch (1976), and Vislobokova (1990) with some modifications. The generally accepted terminology of dental and antler morphology is used in the paper (Heintz 1970; Lister 1987; Vislobokova 1990).

The measurements of tooth rows are taken as maximal possible value; it permits to estimate the functional length of tooth row, which is important for the evolutionary and morpho-functional approach. The measurements of isolated teeth are taken as maximal oral-caudal crown length (L; often it corresponds to the length of grinding surface of a tooth), and lingual-labial breadth of the crown (D; maximal basal breadth for upper cheek teeth; maximal breadth for lower cheek teeth). The specific and little known terminology for dental and antler morphology proposed in some recent publications is avoided, since it overloads the description with specific terminology, which does not bring diagnostically important details. In some cases, the used by authors in the original publications different terminological systems are indicated as analogous names of the same morphological characteristic.

The **cranial measurements** used in the present work (Fig. 1):

1. The condylobasal length of skull (CBL): the measurement is taken from the prosthion point to the posterior edges of the occipital condyles.
 - 1a. The condylodental length of skull (CBD): the measurement is taken from the anterior edge of P² alveolus to the posterior edges of the occipital condyles.
2. The length of upper tooth row (L P²-M³): the measurement is taken from the anterior edge of P² crown to the posterior edge of the M³ crown.
3. The length of upper molar series (L M¹-M³): the measurement is taken as the maximal value (from the anterior edge of the M¹ crown to the posterior edge of the M³ crown).

4. The length of upper premolar series (L P²-P⁴): the measurement is taken as the maximal value (from the anterior edge of the P² crown to the posterior edge of the P⁴ crown).

5. The length of anterior part of the skull before the tooth row (L P²-Pr): the distance between the anterior edge of alveolus of P² and the prosthion point.

6. The length of the posterior part of skull (LPs): the distance between the anterior edge of alveolus of M³ and the posterior edge of the occipital condyles.

7. The length of braincase (LBr): the distance between the bregma point and the opisthocranium.

8. The occipital breadth (DOcp).

9. The occipital height (HO): measured from the basicranium to the opisthocranium.

10. The breadth of occipital condyles (DOC).

11. The length of face (LF): measured from the anterior edge of orbits to prosthion.

12. The length of anterior part of skull (LAnt): measured from bregma to the prosthion.

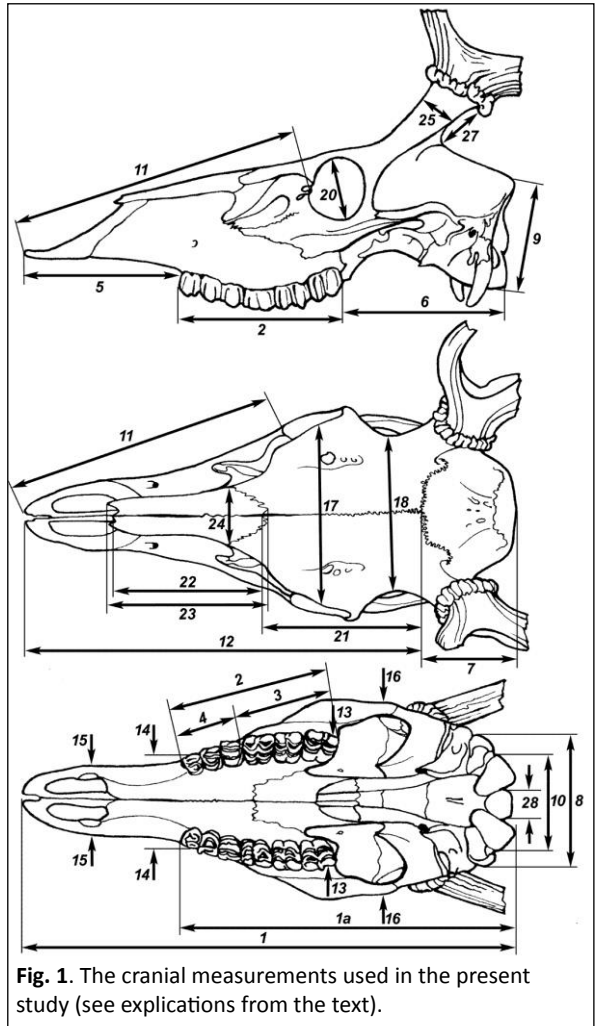
13. The skull breadth at M³ (DMM): the measurement is taken between the alveolar edges in the middle of the right and left M³.

14. The skull breadth at P² (DPP): the measurement is taken between the alveolar edges in the middle of the right and left P².

15. The breadth of muzzle (DMz): the measurement is taken behind upper canines or behind the suture between maxillary and premaxillary bones.

16. The maximal breadth at zygomatic arches (DZg).

17. The breadth above orbits (DO): the measurement is taken above the orbital centres.



18. The frontal breadth (DFr; in males only): the measurement is taken at the frontal constriction before pedicles.
19. The breadth of neurocranium (DNr): the measurement is taken behind the pedicles at males and as a maximal breadth of braincase at females.
20. The diameter of the orbit (DOrb; vertical).
21. The length of the frontal suture (LFr): from bregma to nasion.
22. The length of the nasal suture (LNas): from nasion to rhinion.
23. The maximal length of the nasal bones (LNmax).
24. The breadth of the nasal bones (DNas)
25. The anteroposterior diameter of the pedicle (DAPpd): measured at the upper part of the pedicle.
26. The lateromedial diameter of the pedicle (DLMpd): taken as the previous measurement.
27. The height of the pedicle (Hpd): the lesser measurement taken at the posterolateral side of pedicle.
28. The breadth of the foramen magnum (DFM).

The **measurements of the lower mandible** used in the present work (Fig. 2):

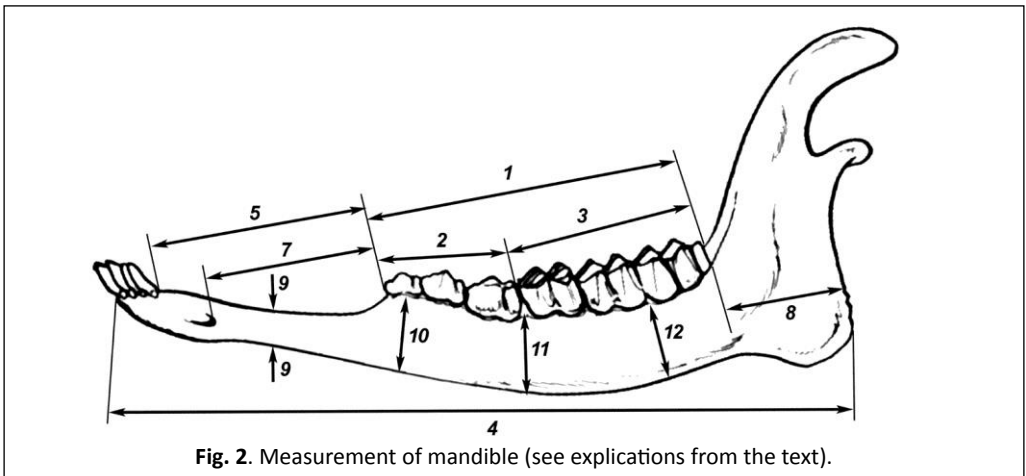


Fig. 2. Measurement of mandible (see explanations from the text).

1. The length of the lower tooth row (L P₂-M₃): the measurement is taken from the anterior edge of P₂ crown to the posterior edge of M₃ crown.
2. The length of the lower premolar series (L P₂-P₄): the measurement is taken as the maximal value (from the anterior edge of the P₂ crown to the posterior edge of the P₄ crown).

3. The length of lower molar series (L M_1 - M_3): the measurement is taken as the maximal value (from the anterior edge of the M_1 crown to the posterior edge of the M_3 crown).
4. The length of the horizontal mandibular ramus (LHR): measured from infradentale (alveolar edge between the first incisives) to the posterior edge of the processus angulatus (angulus mandibulae).
5. The length of the diastema (L P_2 -C): measured from the anterior edge of alveolus of P_2 to the posterior edge of the alveolus of the lower canine (C).
6. The distance between P_2 and the mandibular symphysis (L P_2 -Sym): measured from the anterior edge of the alveolus of P_2 to the symphysis of the mandible.
7. The distance between P_2 and the foramen mentale (L P_2 -FM): measured from the anterior edge of the alveolus of P_2 to the foramen mentale.
8. The distance between M_3 and the posterior edge of the mandible (L M_3 -Post): measured from the posterior edge of M_3 to the posterior edge of the processus angulatus.
9. The height of the diastema (HD): the height of the lowest part of the mandible between P_2 and C.
10. The height of mandible below P_2 ($H \setminus P_2$): the height of the horizontal ramus of mandible is taken as the distance from the anterior edge of alveolus of P_2 to the point on the lower edge of the mandible below P_2 (the taken measurement is perpendicular to the lower edge of the mandible).
11. The height of the mandible below M_1 ($H \setminus M_1$): the height of the horizontal ramus of the mandible is taken as the distance from the alveolus of M_1 in the middle to the point on the lower edge of the mandible (from the lingual side).
12. The height of the mandible below M_2 - M_3 ($H \setminus M_2$ - M_3): the height of the horizontal ramus of the mandible is taken as the distance from the alveolar edge between M_2 and M_3 to the point on the lower edge of the mandible (from the lingual side).
13. The mandibular thickness below P_2 ($D \setminus P_2$).
14. The mandibular thickness below M_1 ($D \setminus M_1$).
15. The mandibular thickness below M_2 - M_3 ($D \setminus M_2$ - M_3).

The measurements are consistent with the craniodental variables used by Janis (1990) for body mass predictions for cervids that is applied in the present study for the ecomorphological description of the fossil forms. The estimated body mass of the fossil deer is calculated as a rounded sum of the obtained body mass predictions based on different cranial and dental measurements.

The antler morphology for small-sized deer is described in accordance to the terminology applied by Heintz (1970) and Lister (1987): the first or basal tine is situated

on the anterior side of the beam close to the burr (in the case of the red deer *Cervus elaphus*, we recognise the first brow and the second bez tines); the next tine situated on the anterior side of the middle part of the beam is called here as middle tine (the trez tine in *Cervus*); the tine situated on the posterior side of the beam is a posterior tine; the distalmost antler branches are called crown tines. The height of the first antler ramification usually is taken from the lateral side; except for the case if the antler beam is curved, when the height of ramification is taken from the convex side of the beam. Similarly, the length of segments (parts of antler beam between two ramifications) is measured from the convex side of the beam. The total antler length is measured along the antler beam from the burr to the distalmost antler tine.

Several nomenclatural schemes designating the antler tines and other morphological elements in antlers of large-sized deer (genera *Praemegaceros*, *Eucladoceros*, *Megaloceros*) are proposed in the literature (Kahlke 1956; Radulesco & Samson 1967; Azzaroli & Mazza 1992, 1993; Croitor 2006b). The idea of homology of antler tines in different genera (Kahlke 1956; Azzaroli & Mazza 1992) is helpful, since it could serve as a handy tool in the reconstruction of phylogenetic relationship among extinct cervid genera. The applied in the present work terminology is largely based on the previous terminological systems with some modifications (Croitor 2006b): the antler tine situated just above the burr is called here the subbasal tine (= tine A: Kahlke 1956; = tine 1; Radulesco & Samson 1967; = spurious tine: Azzaroli & Mazza 1992); the second proximal tine situated on the medial side (or dorsal, if the antler is oriented in the natural position on skull) of the beam is called the dorsal tine (= tine E: Kahlke 1956; = tine 2: Radulesco & Samson 1967; = outer tine in *Praemegaceros*, = inner tine in *Eucladoceros*: Azzaroli & Mazza 1992); the third proximal tine situated on the anterior side of beam is called here the basal tine (= outer tine in *Eucladoceros*: Azzaroli & Mazza 1993); the fourth tine situated on the anterior side of the beam is called here the middle tine (= tine M: Kahlke, 1956; = tine 3: Radulesco & Samson 1967; = anterior tine: Azzaroli & Mazza 1993); the tine inserted on the posterior side of the beam is called here the posterior tine (= tine 4: Radulesco & Samson 1967); the tines situated above the posterior tine are called the crown tines. The nomenclatural schemes for each type antlers is maintained in the present study for two reasons: first of all, the homology of antler tines in different cervid lineages is not proven, so the unification of nomenclatures may cause a false impression of their homological nature. Besides that, the preservation of the already used in the literature nomenclatural schemes permits us to avoid terminological confusions.

The abbreviation used in the present study for deer antlers:

1) for red deer *Cervus elaphus* and related species: **br.**, brow tine; **bz.**, bez tine; **tr.**, trez tine; **cr.**, crown tines;

2) for genus *Praemegaceros*: **sb.**, subbasal tine; **b.**, basal tine, **ds.**, dorsal tine; **m.**, middle tine; **p.** posterior tine; **cr.**, crown tine; **pl.**, palmation.

3) for the most of cervids with complicated antlers the general scheme is used: **b.**, basal tine; **m.**, middle tine; **p.**, posterior tine; **cr.**, crown tine; **ap.**, accessory prong. For

small two or three tined antlers a simple indication is applied: the first (basal, anterior) tine, the second tine (anterior tine of the distal fork), and the third tine (posterior tine of the distal fork).

Morphological criteria of a genus. The attempts of Pfeiffer (1997) and Di Stefano & Petronio (1997) to apply the postcranial morphology in the systematical study of the cervid genera and subgenera gave contradictory and mutually exclusive results (Croitor 2006a). The limb bones in ruminants are influenced by environmental and biomechanical factors and have a minor interest for the systematic study at the genus and subgenus level (Vislobokova 1990). The postcranial morphology depends on the species ecology and locomotion strategy, the landscape character and the body weight (Flerov 1952; Köhler 1993; Croitor 2006a; 2014). The cranial morphology (except for such exosomatic parts as premaxillary bones, preorbital fossae, and relative size of tooth row) provides a set of plesiomorphic characters that have a taxonomic value for the genus level in the systematics of the actual and fossil deer (Pokock 1942, 1943a, b, c; Flerov 1954; Sokolov 1959; Janis & Skott 1987; Vislobokova 1990): 1) the proportions of facial and neural parts of skull; 2) the shape of parietal bones; 3) the shape and relative length of frontal bones; 4) the position, orientation and length of pedicels; 5) the size, position and shape of orbits; 6) the morphology and size of ethmoidal openings; 6) the position and length of nasal bones; 7) the position and shape of the frontonasal suture; 8) the position of the upper dentition row with respect to orbits; 9) the shape of basioccipitale; 10) the morphology and proportions of the lower mandible (the shape of processus angularis, the angle between horizontal and ascending portions).

The morphology of dentition is more widely used in the systematic research and various authors suggested the following characters as a morphological criteria at the genus level (Schlosser 1924; Pocock 1942, 1943a, b, c; Flerov 1952, 1962; Heintz 1970; Azzaroli 1985; Janis & Skott 1987; Vislobokova 1990): 1) the angle between labial and lingual slopes of upper molars, which is correlated to the tooth crown height; 2) the presence or absence of upper canines; 3) development of *Palaeomeryx* fold or presence of its traces. The molarization of lower fourth premolar (P_4) and the length ratio between lower premolar and molar series are often used as morphological criteria of genus in cervid systematics (Vislobokova 1990).

Janis & Lister (1985) described a rather high individual variation of P_4 in pecorans and suggested a cautious implication of this character in taxonomy studies. The high morphological variation of P_4 is shown for *Cervus elaphus* with frequency of low molarization from 8 % to 47 % in different populations. P_4 seems to be quite rather variable in the subfamily Cervinae, although the high molarization of P_4 seems to be rather constant in the genus *Dama*. The variability of molarization of P_4 itself may be regarded as a species specific character. This character is more constant in the deer of the subfamily Capreolinae. The premolar/molar ratio is broadly used in the characterization of evolutionary specialization within the subfamily Cervinae: generally the relatively short series of premolars represents an advanced evolutionary feature in the plesiometacarpal deer (Vislobokova 1990). This morphological feature

is often evolved in combination with the molarization of P_4 in parallel in the majority of cervine lineages as a result of the increase of the grinding functional component of the cheek tooth row and the diminished cutting function of the tooth row performed only by the lower unmolarized premolars. However, this evolutionary trend is characteristic only for the subfamily Cervinae. The evolutionary pattern of the functional structure of the Capreolinae is some-what different: the praemolar/molar ratio within the subfamily varies very little, while the molarization of lower premolars attains the exceptionally advanced degree (Croitor 2014). P_4 in the most advanced representatives of Capreolinae (*Alces*, *Rangifer*) evolves into a functional analogue of molar, while P_3 also evolves a certain degree of molarization, thus ensuring the increase of the grinding function of the lower cheek tooth row. Therefore, in the case of each cervid species, the taxonomical significance of some characters (molarization of P_4 , molar/premolar ratio, and some other cranial and dental characters) should be estimated according to other craniodental correlated characters and the broader systematical context.

The implication of the antler morphology in the systematics of genera is restricted only to the general bauplan of the antler construction shared by several species. The morphological criteria of the genus level provide information on the evolutionary history of the Cervidae after the main (Late Miocene – Pliocene) evolutionary radiation of the so-called “crown deer” or/and a specific rapid evolution under the exceptional pressure of environmental conditions.

Morphological criteria of a species. The species description is based on the exosomatic characters influenced by the intraspecific social interactions and environmental factors (Azzaroli 1953, 1992; Flerov 1952; Vislobokova 1990; Geist 1998). The cranial and dental characters of the species rank are the following: 1) the relative length of muzzle (premaxillary length and length of diastema); 2) the shape of premaxillary bones; 3) the length of nasopremaxillary suture; 4) the size and degree of development of preorbital fossae; 5) the size and shape of bullae tympani; 6) the shape and relative length of frontal appendages (pedicles); 7) the development of the cingulum, the *Palaeomeryx* fold and other additional enamel folds; 8) the ratio between premolar and molar tooth series length; 9) the molarization of lower fourth premolar (P_4). The species-level morphological features generally characterize the ecological niche of species (Pocock 1942, 1943a, b, c; Janis & Skott 1987).

The characters of the antler morphology used in the species systematics: 1) the direction, shape and length of the antler beam; 2) the number of tines; 3) the development of palmation; 4) the reduction of antler tines and the general simplification of antlers.

The proportions of limb bones and body size are used in the species definition only in combination with the above mentioned characters (Flerov 1952).

The detailed taxonomic description is provided only for species with revised or modified taxonomic status.

Late Neogene and Quaternary geochronology. The updated geochronological timescale ratified by the International Union of Geological Sciences in 2009 is used in the present work. According to the updated timescale, the lower boundary of the Quaternary period and the Pleistocene epoch boundary are lowered until the base of the Gelasian Age at 2.58 Ma (Gibbard & Head 2009; Gibbard et al. 2010). The Miocene/Pliocene boundary is established at 5.3 Ma (Steininger et al. 1989).

The biochronologic unit subdivision of the geological time scale into Mammal Neogene Faunal Zones (MN) is a broadly accepted biostratigraphic scale based on the European mammal paleontological record (Mein 1989). The biological events within the updated MN zones are fixed at the genus level with indication of first and last occurrences of genera; each MN zone is characterized by a list of main genera (Mein 1989). As Azzaroli (1992) noticed, the Mammal Zones of Mein lack flexibility needed for alterations and refinement with progress of paleontological knowledge. Nonetheless, the MN zones as a universal time scale for European bioprovince represent a very handy tool when researchers are dealing with isolated fossiliferous sites that cannot be connected to well-defined stratigraphic sections or are preserved without geological time indication, as, for instance, fissure and cave fillings (Schmidt-Kittler 1989).

The parallel European biochron system comes from the old paleontological tradition and is based on well-known local or regional faunas. These Plio-Pleistocene mammal faunal units of Europe represent a larger scale biochron system: the Ruscian (MN14-15) and the Villafranchian (MN16-17) characterize the faunal evolution of the Southern Europe during Pliocene and Early Pleistocene correspondingly (Steininger et al. 1989). Rook & Martinez-Navarro (2010) define the Villafranchian as a Mammal Age based on the South European paleontological record analogous to the mammal ages commonly used in North America. The Villafranchian (from around 3.5 Ma to about 1.0–1.1 Ma) is considered as a useful tool for large scale regional and continental chronological correlations (Rook & Martinez-Navarro 2010). Bellucci et al. (2015) regard Epivillafranchian (1.2-0.9 Ma) as a self-contained biochron defining a transitional stage between the Villafranchian and the Galerian. The Galerian Mammal Age, according to Bellucci et al. (2015), includes the faunal units Ponte Galeria, Isernia, and Fontana Ranuccio, ranging from 0.8-0.75 Ma to ca. 0.5 Ma (Gliozzi et al. 1997; Petronio & Sardella 1999). The European Plio-Pleistocene Mammal Ages are based on the Italian and French paleontological record, however, some of them (the Ruscian and the Villafranchian) are applied also to the Eastern Europe and Northern Asia (Pevzner et al. 1996; Vangengeim et al. 2005, 1998). The Ruscian, the Villafranchian and the Galerian are applied in the present work as convenient terms defining the paleobiogeographic affinity of fossil cervid forms, in particular in the cases when their exact age or stratigraphic provenance are unknown.

SYSTEMATIC DESCRIPTION

FAMILY CERVIDAE GOLDFUSS 1820

SUBFAMILY CAPREOLINAE BROOKES 1828

Genus *Procapreolus* Schlosser 1924

The genus *Procapreolus* was proposed by Schlosser (1924) for small to medium sized deer with three-pointed antlers similar to those of modern roe deer: *Cervus (Palaeaxis) loczyi* Pohlig, 1911 from Late Miocene of Pannonia, *Cervavus rutimeyeri* Schlosser 1903 (= *Procapreolus rutimeyeri*: Schlosser 1924) and *Procapreolus latifrons* Schlosser, 1924 from Late Neogene of Mongolia.

Korotkevich (1963, 1965b), the first reviewer of the genus, designated *Procapreolus latifrons* as the type species and excluded *Cervavus rutimeyeri* from *Procapreolus*, since the shape of its antlers did not correspond to the new diagnosis of the genus. Korotkevich (1963) also ascribed to *Procapreolus* the dental remains from Late Tertiary of China described by Schlosser (1903: 118) as *Cervavus* sp. 2. This cervid form is characterized by the primitive P_4 (Schlosser 1903: tab. X, fig. 14) and the presence of protoconal fold in M^3 . According to Dong & Ye (1997), *Procapreolus latifrons* is a random variation form of "*Cervavitus novorossiae*" from China. Thus, the taxonomical context of *Procapreolus* becomes confused because of the uncertain taxonomical status of its type species and the unclear systematical position of Asian cervid remains described as "*Cervavitus novorossiae*" (Czyżewska 1968; Azzaroli 1992; Di Stefano & Petronio 2002). The suspended taxonomical context caused a cautious use of the genus name *Procapreolus*, which is potentially polyphyletic in its current understanding (Croitor & Stefaniak 2009; Croitor 2014).

Procapreolus latifrons (the estimated body mass is ca. 35 kg) was based on a complete frontal bone with a proximal fragment of antler characterized by the thin beam (diameter amounts to 25 mm) and the comparatively high position of the first ramification (ca. 95 mm above the burr). The frontal bone is broad (the breadth of the frontale amounts to 45 mm) and flat, the pedicle is slightly compressed anteroposteriorly and is relatively long. The section of the beam is nearly circular (Schlosser 1924). Schlosser (1924) ascribed to *P. latifrons* some large upper canines (at list, 50 mm of length) and lower mandibles with molarized P_4 . Lower molars are supplemented with ectostylids and an anterior enamel "fold of compression". The *Paleomeryx* fold is not present in lower molars (Schlosser 1924). In my opinion, the type specimen described by Schlosser (1924) and the additional material represented by the antlered braincase (Zdansky 1925: pl. VI) and the antler fragments from the *Hipparion* fauna of China (Schlosser 1903: pl. XI, fig. 30; Zdansky 1925: pl. 5, fig. 5) display stable morphological characters and show the clear affinity with the capreoline deer from Late Miocene and Pliocene of Europe. Therefore the genus name *Procapreolus* with the type species *P. latifrons* should be maintained in the sense proposed by Korotkevich (1963).

Korotkevich (1965) proposed to exclude *Cervavus rutimeyeri* Schlosser 1903 from the genus *Procapreolus* because of the antler shape that is quite different from that of *P. latifrons*. *Cervavus rutimeyeri* Schlosser 1903 (estimated body mass 34 kg) was based on relatively larger upper molars from Late Tertiary of China, characterized by well-developed basal structures (cingulum), and strong inner folding of hypocone in P³ and P⁴; its lower molars have no *Palaeomeryx* fold (Schlosser 1903: tab. X, figs. 1-5). Later, Schlosser (1924) included this species in his new genus *Procapreolus* and tentatively ascribed as *Procapreolus* cf. *rutimeyeri* some antler remains from Late Tertiary of Mongolia, which are distinguished from *P. latifrons* in a more flattened antler beam, a higher position of the first tine (which is smaller and weaker), and a stronger posterior tine of the distal bifurcation, which represents a beam continuation. There is a prominent anterior crest between the first tine and the burr, while the posterior side of the beam is flattened, therefore the transversal section of beam is nearly triangular (Schlosser 1924). The beam segment between the first and second bifurcations has also an irregular cross-section because of the posterior rib and more flattened anterior side of the beam above the basal tine (Schlosser 1924: fig. 4-b). The antler part in the area of the second ramification is moderately flattened. The antler length attains 180 mm, while the burr diameter varies between 25 and 30 mm (Schlosser 1924). The pedicle has a circular cross-section, with the position on the skull as in modern *C. capreolus*, but relatively longer (Schlosser 1924). The enlisted antler characters show a great affinity with *Pliocervus matheroni* from the Late Miocene of Cucuron (France), therefore I agree with the opinion of Korotkevich (1965) that *Cervavus rutimeyeri* should be excluded from the genus *Procapreolus*.

The taxonomic status of *Procapreolus loczyi* (Pohlig, 1911) from the Late Miocene of Hungary is unclear too. Korotkevich (1965b) and Czyżewska (1968) suggest that the antler shape of *Cervus (Palaeaxis) loczyi* shows an affinity with *Pliocervus*. The fragmentary antler remains described by Pohlig (1911) as *C. (Palaeaxis) loczyi* are quite poor, but hardly show any affinity with *Pliocervus*: the best preserved shed antler is at list three-tined; the first tine is situated rather high on the beam, but somewhat closer to the burr than to the second ramification. The antler is slightly compressed from the sides and reminds *Cervavitus novorossiae*. One of the pedicles figured by Pohlig (1911) is thin and long, but another pedicle connected to a small part of the antler is rather short and robust. The figured specimens come from various localities and most probably belong to different cervid forms.

The genus includes up to nine species from Late Miocene to Early Pleistocene of the middle latitudes of Eurasia, four of which come from the Pliocene of Western Eurasia.

PROCAPREOLUS MOLDAVICUS (JANOVSKAYA, 1954)

This is the largest species of *Procapreolus* with the estimated body mass about 40-50 kg. Janovskaya (1954) described the species *Cervus (Rusa) moldavicus* from Pliocene of Moldova, assuming the transitional phylogenetic position of the new species between Late Miocene *Cervavitus* and the modern genus *Cervus*. Croitor (1999) included this species in the genus *Procapreolus* and synonymized *Procapreolus moldavicus* with

Cervocerus wenzensis Czyzewska, 1960 from the Early Pliocene of Węże-1 (Poland). *Muntiacus flerovi* Pidoplitschko, 1951 is another junior synonym of *P. moldavicus* (Korotkevich 1970; Croitor & Stefaniak 2009).

The poorly preserved antlers from Early Pliocene of Kuchurgan (Ukraine) described by Korotkevich (1965) as *Pliocervus kutchurganicus* fall within the range of individual variation of the sample from Węże-1 and therefore *Pliocervus kutchurganicus* is regarded as a junior synonym of *Procapreolus moldavicus* too (Croitor & Stefaniak 2009). A part of antlers from Kuchurgan were reported by Korotkevich (1970) as *Procapreolus cf. cusanus*, however the cited author failed to demonstrate the presence of two species in the dental and postcranial material from Kuchurgan. Apparently, this taxonomical confusion between *Procapreolus* and *Pliocervus* is caused by the poor and vague definition of the type species of the genus *Pliocervus*, *Cervus matheroni* Gervais, 1859 from the Late Miocene of France (Croitor 2014). Unlike *Procapreolus*, *Pliocervus matheroni* is characterized by massive pedicles with more or less parallel orientation; the distance between pedicles is small as in *Capreolus*, differing from the broad spaced pedicles of *Procapreolus*. The fully developed antlers of *Pliocervus matheroni* are four-

pointed with an irregular subtriangular cross-section of the beam and triangular cross-section of tines, unlike regularly circular cross-sections of beam and tines in the most of the *Procapreolus* species, or oval cross-sections of flattened tines in *Procapreolus cusanus*. None of the antlers from Kuchurgan corresponds to the diagnostic characters of *Pliocervus*. Finally, the lower fourth premolar (P_4) of *Pliocervus matheroni* is primitive, unlike highly molarized P_4 in *Procapreolus* (Croitor 2014). The fine complete antlers from the Pliocene sites of Czorna Loszczina and Andreevka (South Ukraine) described by Korotkevich (1964) and Korotkevich (1970) as *Procapreolus cusanus* (Fig. 3, A) and *Procapreolus cf. cusanus* also belong to *P. moldavicus* (Croitor & Stefaniak 2009).

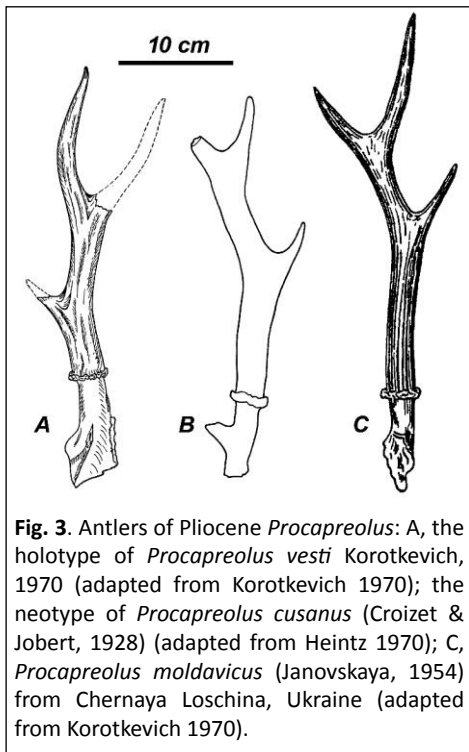


Fig. 3. Antlers of Pliocene *Procapreolus*: A, the holotype of *Procapreolus vesti* Korotkevich, 1970 (adapted from Korotkevich 1970); the neotype of *Procapreolus cusanus* (Croizet & Jobert, 1928) (adapted from Heintz 1970); C, *Procapreolus moldavicus* (Janovskaya, 1954) from Chernaya Loschina, Ukraine (adapted from Korotkevich 1970).

The species holotype is a partial articulated skeleton of a juvenile female (skull, mandible, back bone, os innominatum, posterior limbs) No. 2, PIN (Janovskaya 1954; Croitor 1999). The skull (Nr. 2/1) is partially reconstructed

with plaster, however, the reconstruction is not exact: the skull flexion (angle between facial and cerebral parts) is not maintained, the orbitofrontal part of the skull is artificially lengthened (the two parts of the preserved right zygomatic arch do not coincide and the gap between them is ca. 13 mm); the axe of braincase is somewhat offset leftward

(Croitor 1999). The braincase is heavily damaged; only parietals and right temporal bones are preserved. The left side of the face is also damaged; both premaxillary bones are present, however, their contact with the rest of the skull is not preserved. The frontal-orbital part of the skull is short: the anterior edge of the orbits is situated above M^2 . Frontal bones are flattened, with sharp supraorbital channels ranging from pedicle base to the level of preorbital fossae. The preorbital pit is quite deep (ca. 1 cm) and large (21.0×12.0 mm). The preorbital pit is more sharply outlined and just slightly smaller than of a female of modern *Muntiacus muntjak* (22.7×14.3 mm). The nasal bones are short and do not reach the line connecting the anterior edges of the orbits. The mandibular diastema is relatively short (shorter than in *Capreolus*). The dentition consists of fully functional deciduous teeth, functional first and second upper and lower molars, and third molars in process of eruption. Additional measurements: skull breadth at PD^4 amounts to 66.0 mm; skull breadth at PD^2 , 35.2 mm; skull breadth at M^2 , 34.0 mm; palatal breadth between M^2 , 34.0 mm; length of the right upper tooth row (PD^2 - M^3), 70.4 mm; length of the right upper molars (M^1 - M^2), 41.5 mm; length of the right upper deciduous teeth (PD^2 - PD^4), 34.2 mm.

The type specimen comes from the environments of Fagadâl, nowadays the southern part of Lebedenco village (= Făgădău, = Fagadil, = Fagadyl: Khomenko 1917; Janovskaya 1954; Croitor 1999; Vislobokova 2008), Cahul District, Moldova. The fossil remains were yielded by the Early Pliocene of the Carbolian alluvium (MN15).

The additional material from the Carbolian alluvium (IZC), Węże-1 (IZW), and Kuchurgan (MNHK) provide some more details on species morphology. The preorbital fossa in males are very large and deep, with sharp edges. The largest diameter of the preorbital fossa in the male skull from Węże-1 (Fig. 4) amounts to 29 mm and attain ca. 74% of the orbital diameter. The relative diameter of the preorbital fossa in *P. moldavicus* is somewhat smaller than in *Muntiacus* (the relative size of preorbital fossa to the orbit diameter is 81.4 % in *M. muntjak* and 99 % in *M. reevesi*). The depth of the preorbital fossa is 10.4 mm. The size of ethmoidal openings equals the diameter of orbits.

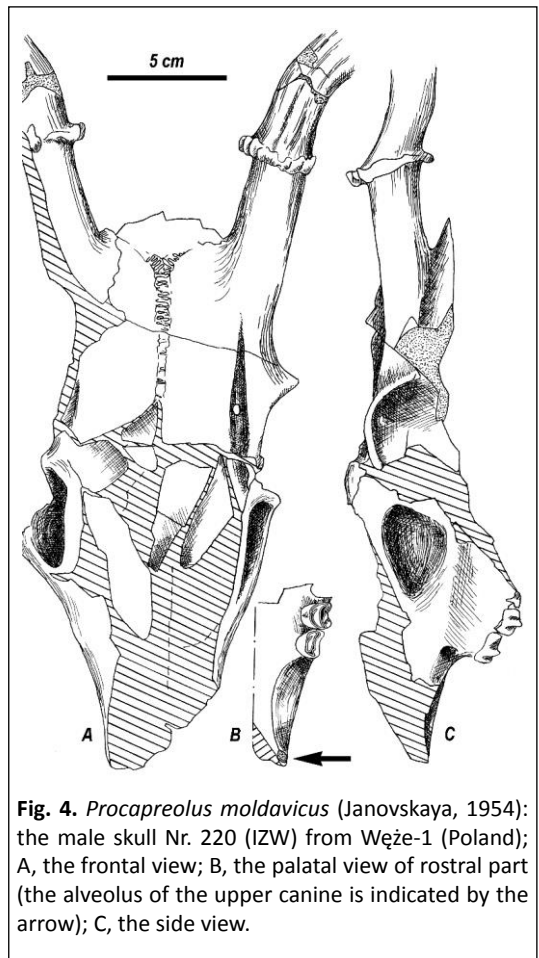


Fig. 4. *Procacpreolus moldavicus* (Janovskaya, 1954): the male skull Nr. 220 (IZW) from Węże-1 (Poland); A, the frontal view; B, the palatal view of rostral part (the alveolus of the upper canine is indicated by the arrow); C, the side view.

The pedicles are very long: their length measured on the medio-posterior side is always higher than the pedicle diameter, strongly sloped backward from the face (the angle between pedicles and parietal bones is about 50° and oriented slightly laterally, so the angle between pedicles is about 30°. The strong inclination of the pedicles is the same as at *Pavlodaria orlovi* (Flerov, 1950) from late Miocene of Western Siberia (Vislobokova 1980, 1990) and *Procapreolus cusanus* from Pliocene of France (Heintz 1970: pl. 1, fig. 1a), whereas the pedicles in *Eocoileus gentriorum* Webb from Pliocene of North America (Webb 2000), modern *Odocoileus* and *Capreolus* are in a more vertical position, with the angle between pedicles and parietals amounts to 68°. The large distance between somewhat divergent pedicles approaches *P. moldavicus* to modern *Odocoileus* and distinguishes it from *Capreolus* (Fig. 5). The male skull Nr.220 from Węże-1 and female skull from Fagadâl show that the nasal bones are rather short, like in *Odocoileus* and *Muntiacus*, and do not reach the level of orbits as in *Capreolus*. The length of supraorbital channel in the specimen Nr. 220 from Węże-1 amounts to 58 mm. At females, the supraorbital channel is weak and visible only above the orbits, its length measured on the female skull Nr. 345 amounts to 37 mm. The supraorbital channel has a parallel orientation with respect to the interfrontal suture and is expressed stronger than those in *Capreolus* and Pliocene *Pavlodaria* from Kazakhstan.

Upper canines at males are moderately large: the anteroposterior diameter of the right canine alveolus on the male skull Nr. 220 attains 6.2 mm. The distance between canine and P² is 35.4 mm. The upper molars are characterized by the presence of a large protoconal fold and a hypoconal spur, like those of modern *Odocoileus virginianus*. The lingual side of molars is strongly inclined in *P. moldavicus*, the angle between labial and lingual sides of the upper molar amounts to 55°. The entostyle is variable. The lingual wall of P² is not cleft and does not show a vertical groove. Its hypocone is supplemented by an internal enamel fold. The lingual side of P³ is grooved. The hypocone is characterized by an internal enamel fold that may disappear in heavily worn teeth. Additional internal enamel folds may occur in both protocone and hypocone of the P⁴. Those enamel folds may disappear in teeth with advanced degree of wear.

The P₄ is always molarized: its metaconid extends anteriorly and is fused with the paraconid. The entoconid is not connected with the entostylid. The length ratio between the lower premolars and molars varies from 62.6 to 65.7% (n = 4) in the sample from Węże-1. The lower premolar series at the specimen from Musait (IZC, Moldova) is relatively longer, with the premolar/molar length ratio amounting to 70.6 %. Lower molars are characterized by the development of ectostylids. The *Palaeomeryx* fold is rather variable: it is well expressed in the holotype from Fagadâl, but quite poorly developed in the lower mandible from Musait (Croitor 1999). The broad variation of the *Palaeomeryx* fold development is observed in the sample from Węże-1. The *Palaeomeryx* fold is represented by a weak vestige in the specimen Nr. 220, but it is recorded at 69 % of specimens from the sample (11 of 16 specimens). The *Palaeomeryx* fold is stronger and more often developed in M₁. The development of ectostylids in M₃ is a variable character too: M₃ may have both anterior and posterior ectostylids (the specimen Nr. 248 from Węże-1), or possesses only the anterior ectostylid as at the specimen Nr. 220 from Węże-1.

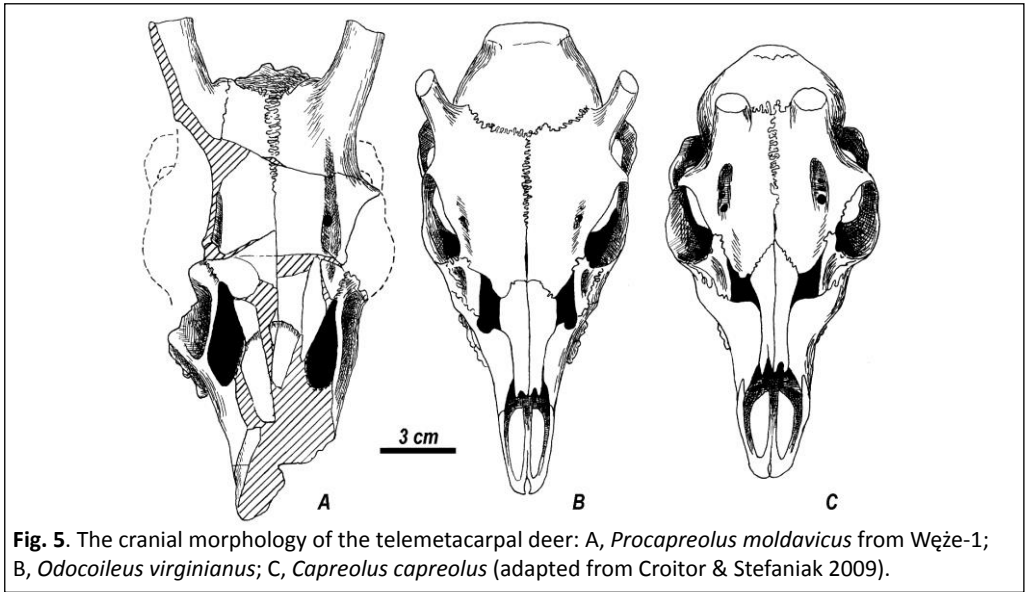


Fig. 5. The cranial morphology of the telemetacarpal deer: A, *Procapreolus moldavicus* from Węże-1; B, *Odocoileus virginianus*; C, *Capreolus capreolus* (adapted from Croitor & Stefaniak 2009).

The dental measurements of *P. moldavicus* are close to those of *Croizetoceros ramosus*, however they differ from the latter form by a set of primitive characters, such as the broader crowns of the upper molars, the relatively longer lower premolar series, and the presence of the *Palaeomeryx* fold in the lower molars (Croitor & Stefaniak 2009).

The antlers are always three-pointed, long, and thin. The recorded antler length for an adult individual from Czorna Loszczina amounts to 309 mm (Korotkevich 1964). The antler beam is straight or undulated in its basal part (Czyżewska 1960; Korotkevich 1964; Croitor 1999). The transverse section of the basal portion of the antler beam is circular. In many cases, the antler beam becomes somewhat compressed distally with a flat lateral side and a convex medial side. The antler is strongly compressed in the latero-medial direction in the areas of the first and the second bifurcation, however, the beam segment between the first and the second ramifications is never flattened as in *P. cusanus*. The first tine is situated very high, almost at 1/2 antler length. The first tine is very short at young individuals, and much longer at fully developed antlers. The anterior tine of the distal bifurcation is a continuation of the beam. The antler surface is ornamented with ridges and furrows.

The antlers of the specimen Nr. 220 (IZW) from Węże-1 are thin, with the antler base inclined backward from the burr and then curved toward the anterior and the sides, reminding the “S-shaped” morphological condition of “*Pliocervus kutchurganicus*”. The antler becomes compressed in the latero-medial direction in the area of the first tine. On the anterior side, the antler beam has a rather deep groove that is continued on the anterior side of the first tine. This remarkable anterior groove is regarded by Korotkevich (1970) as a diagnostic character of “*Pliocervus kutchurganicus*”. The transverse section of the beam above the first tine is circular. The distal portion at fully developed antlers is significantly compressed from the sides in the area of the distal bifurcation, as

one can see on the specimens W-328 and W-329. The proximal antler fragments Nr. 324 (DLM above burr is 26.5 mm) and Nr. 364 (measurements are unavailable) are somewhat more robust and straight unlike the specimen Nr. 220 (DLM above burr is 22.0 mm). Therefore, the type specimen of "*Pliocervus kutchurganicus*" (DLM above burr amounts to 31.2 mm) represents a variant of antler shape represented also in the sample from Węże-1, while the size of antlers from the Polish sample falls within the size range of antlers from Kuchurgan described by Korotkevich (1970) as "*Pliocervus kutchurganicus*" (DLM above burr: 13.3-31.2 mm).

According to Vislobokova (2008), the species *Cervus (Rusa) moldavicus* is doubtful since its type specimen is represented by a juvenile female and does not provide such diagnostic characters as the antler morphology and the permanent premolar morphology. Vislobokova (2008) proposes to regard Janovskaya's deer as *Procapreolus* sp. and uses *Procapreolus wenzensis* (Czyżewska, 1960) to designate the Early Pliocene archaic Capreoline deer from Eastern Europe. Vislobokova (2008) also supports the validity of *Pliocervus kuchurganicus* Korotkevich, 1965 and mentions *Procapreolus cusanus* (Croizet & Jobert, 1828) in composition of the fauna from Kuchurgan. The debate on the priority of scientific names initiated by Vislobokova (2008) is unnecessary, since the fossil remains from Węże-1 also contain cranial remains of juvenile females (including the fine skull Nr. 345 chosen as the paratype of *Cervoceros wenzensis* by Czyżewska 1960), which morphologically are identical to the holotype of *Procapreolus moldavicus* (Croitor & Stefaniak 2009). The claimed by Vislobokova (2008) antler morphology as a missing diagnostically important information, is not much helpful for the species definition in this case, since antlers within the genus *Procapreolus* are uniform and, except for fully developed antlers of *Procapreolus cusanus*, do not provide secure diagnostic characters. Species of the genus *Procapreolus* are distinguished by the details of the dental morphology, such as the development of *Palaeomeryx* fold in lower molars and the presence of cingulum in the upper molars (Korotkevich 1970, 1974). The upper and lower molars of the holotype of *Procapreolus moldavicus* provide the necessary diagnostic characters for the species definition and its differential diagnosis. *P. moldavicus* is significantly larger than *P. florovi* and *P. vesti*, which are characterized by the similar dental and antler morphology. It is distinguished from *P. graecus* by the larger size and the presence of the *Palaeomeryx* fold in the lower molars. Unlike *P. ucrainica*, the upper molars of *P. moldavicus* have no cingulum; *P. moldavicus* is distinguished from *P. cusanus* by its larger size, the presence of *Palaeomeryx* fold in the lower molars, and the thin long antlers that never develop flattened palmations and additional crown tines.

PROCAPREOLUS PENTELICI (DAMES, 1883)

Synonymy:

1862 *Dremotherium* sp.: Gaudry, p. 308

1867 *Dremotherium* sp.: Gaudry, pl. LVI, fig. 7

1883 *Cervus pentelici* nov. sp.: Dames, p. 93, pl. V, fig. 1.

1898 *Capreolus pentelici* (Gaudry): Trouessart, p. 889.

1968 *Pliocervus pentelici* (Caudry): Melentis, p. 4, pls. 4-5.

1995 *Pliocervus graecus* n. sp.: Azanza, p. 158, pl. 1, fig. 2.

2017 *Procapreolus cusanus* (Croizet & Jobert): Cregut-Bonneure & Tsoukala, fig. 7.

Holotype: the pair of antlers 1967/18 of an adult individual (Dames 1883; Melentis 1968) stored in the paleontological collection of the University of Athens. Antlers are long, thin, three-pointed; the posterior tine of distal bifurcation of the left antler is flattened and supplemented by a knob interpreted as a primordial accessory tine (Melentis 1968).

Type locality: Pikermi (Greece).

Stratum typicum: Late Miocene (MN12/MN13 boundary).

Distribution: Late Miocene – Pliocene (?); Greece.

Emended diagnosis: The body size is similar to that of the modern European roe deer. Antlers are thin, three-pointed, with circular cross-section of beam. The first tine is situated closer to the distal bifurcation than to the burr. Pedicles are very long: their length measured from the posterolateral side significantly exceeds the diameter of the pedicle. The *Palaeomeryx* fold in lower molars is not present. The cingulum in upper molars is not developed.

Differential diagnosis: *P. pentelici* is distinguished from *P. moldavicus*, *P. vesti*, *P. florovi*, and *P. ucrainica* by the absence of the *Palaeomeryx* fold in lower molars. Unlike *P. ucrainica*, the upper molars of *P. pentelici* have no cingulum. *P. pentelici* is distinguished from *P. cusanus* by thin antlers with the more or less cylinder-shaped beam and tines.

Dames (1883) described the new species *Cervus pentelici* from Pikermi (Greece) on the basis of a well-preserved pair of three-pointed antlers and associated them with a braincase without cranial appendages and a mandible of small-sized cervid and another mandible of larger deer described by Gaudry (1862, 1867) as *Dremotherium pentelici* and *Dremotherium* sp. correspondingly. The remarkable relative difference between the size of dental remains and the large size of antlers were explained by Dames (1883) as a sexual dimorphism. Gaudry (1862, 1873), who studied both samples from Pikermi and Mont Luberon, did not report similarity between Greek and French cervid remains.

Actually, the smaller mandible (PIK2034a, sin; PIK2034b, dx; MNHN, Paris) from Pikermi described as *Dremotherium pentelici* belongs to a muntjac-sized ruminant (L P₂-M₃ amounts to 55.4 and 55.0 mm respectively), while the braincase PIK2020 (MNHN) does not belong to a deer; the collection label associated with the specimen defines it as “*Gazella brevicornis* cf. *capricornis/deperdita*?”. Melentis (1968) included the material described by Gaudry (1862, 1873) and Dames (1883) in Gaudry’s species, which was placed in the genus *Pliocervus*. Azanza (1995) proposed a new species name *Pliocervus graecus* for the deer remains from Maramena (Greece). Azanza (1995) reported a great similarity between the antlers from Maramena and those from Pikermi and confirmed the presence of the second smaller cervid in the fauna from Pikermi that should maintain the species name given by Gaudry: *Dremotherium pentelici*. Azanza (1995) established a new species name *Pliocervus graecus* for larger cervid form in order to avoid the homonymy of species names proposed by Gaudry (1862) and Dames (1883). Actually, species name *Cervus pentelici* Dames, 1883 remains available for the larger cervid from Pikermi characterized by three-tined antlers and is not a homonym of *Dremotherium pentelici* Gaudry, 1862, since those two species names originally were established in combination with different generic names (ICZN, Article 53.3), and the secondary homonymy is improbable. Therefore, *Cervus pentelici* Dames, 1883 is the senior synonym of *Pliocervus graecus* Azanza, 1995.

The antler and dental morphology of the deer from Pikermi and Maramena is typical for *Procapreolus*: three-tined antlers are thin, long (390 mm), with very high position of the first tine, circular cross-section of the beam; pedicles are thin, slightly diverging, with large distance between them; P₄ is highly molarised, not simple as at *Pliocervus matheroni*. The body size of *Procapreolus graecus* (27 kg) is very close to that of *P. florovi* from the Late Miocene of Ukraine. Unlike the latter species, the Greek cervid, as Azanza (1995) reported, lacks *Palaeomeryx* fold in lower molars. The lingual wall of the upper premolars is split by a deep vertical groove, which is stronger expressed than at *P. moldavicus* from Weze. Apparently, *Procapreolus graecus* is very close to *P. florovi*, but somewhat more advanced in its dental morphology. The capreoline remains from the younger Pliocene site of Gephyra (Greece), described by Cregut-Bonnoure & Tsoukala (2017) as *Procapreolus cusanus*, are characterized by the similar to *P. pentelici* and *P. cusanus* size, and, as those two species, lacks the *Palaeomeryx* fold. However, unlike *P. cusanus*, antlers of the deer from Gephyra are thin and not flattened in their distal part. Despite of the significantly younger age (MN16a), *Procapreolus* from Gephyra seems to be closer to *P. pentelici* than to *P. cusanus*.

PROCAPREOLUS VESTI (KOROTKEVICH, 1970)

Synonymy:

1959 *Procapreolus* sp.: Verestchagin, p. 52, figs. 25-5, 25-6.

1959 *Pliocervus* sp.: Verestchagin, p. 52.

1970 *Pliocervus kutchurganicus vesti* ssp. nov.: Korotkevich, p. 133, fig. 48.

1970 *Procapreolus* sp.: Korotkevich, p. 109, fig. 41.

2009 *Procapreolus moldavicus* (Janovskaya, 1954): Croitor & Stefaniak, p. 17, fig. 13-b.

Holotype (Fig. 3, A): the almost complete right antler with pedicle and part of frontal bone Nr. 1 stored in the Zoological Institute, Sankt-Petersburg (Korotkevich 1970). The antler is relatively robust (DLM antler base is 28.4 mm) and belongs to a mature individual. The first ramification is situated approximatively in the middle between burr and the second ramification (L burr - ramification amounts to 108.4 mm; L first - second ramifications amounts to 118.0 mm). The cross-section of antler beam is regularly circular. Pedicle is relatively long (L, 32.0 mm; DLM, 25.6 mm) and slightly compressed anteroposteriorly (DAP, 24.9 mm). The frontal bone has a rather deep, well-outlined and long supraorbital channel.

Type locality. Kosiakinsky Quarry (= Kosiakino: Pevzner et al. 1996), 10 km west of Stavropol (Russia).

Stratum typicum. According to Verestchagin (1959), the fauna from alluvial sands of Kosiakinsky Quarry is close to the fauna from Malușteni (Romania). Pevzner et al. (1996) indicate the mixed character of the fossil remains from this site.

Distribution. Pliocene (MN 15?), North Caucasus foothills (Russia).

Diagnosis. The body size is comparable to that of the modern muntjacs. Antlers are relatively large, three-pointed, with rounded cross-sections of the beam and tines. The antler segment between the first and second ramifications often is elongated. Upper molars have no cingulum. The *Palaeomeryx* fold in lower molars is well-developed.

Taxonomical remarks. A well-preserved shed antler and lower mandible from Kosyakino were figured and mentioned by Verestchagin (1959) as *Procapreolus* sp. Verestchagin (1959) also mentioned *Pliocervus* sp. in the faunal list of Kosiakino, however, he does not indicate the fossil material attesting the presence of this genus in the fauna from Kosiakino. Korotkevich (1964) considers that the material figured by Verestchagin belongs to *Pliocervus*. Later, Korotkevich (1970) described the new subspecies *Pliocervus kutchurganicus vesti* based on a well-preserved antler from Kosyakino that apparently belongs to a mature individual. In the same work, Korotkevich (1970) describes a very thin antler with a short first tine situated at almost equal distance between the burr and the distal bifurcation as *Procapreolus* sp. This specimen was correctly interpreted by Korotkevich (1970) as the antler of young animal. Croitor & Stefaniak (2009) assumed that the material from Kosiakino may belong to *P. moldavicus*, however, the peculiar small body size similar to that of modern muntjacs suggest that we are dealing with another true species of *Procapreolus*.

Procapreolus vesti is the smallest species of the genus (L P₂-M₃ = 58.0 – 73.0 mm; n=3; the estimated mean body mass amounts to 21.5 kg) that represents a particular direction of specialization within *Procapreolus*. Besides its small body size, *P. vesti* is also characterized by the relatively longer antler segment between the first and

second ramifications, although the antler proportions of *P. vestii* broadly overlap with *P. cusanus*. All dental remains from Kosiakino are characterized by the molarized P₄ and the presence of the *Palaeomeryx* fold in the lower molars (Korotkevich 1970). Korotkevich (1970) reported the morphological heterogeneity of the sample from Kosiakinsky Quarry and distinguished larger teeth with stronger *Palaeomeryx* fold that she described as *Procapreolus*, and smaller teeth with weak *Palaeomeryx* fold that, according to Korotkevich, belong to *Pliocervus*. The observed size and morphological variation corresponds to the intraspecific variation and, most probably, confirms the fact that the sample from Kosiakino chronologically is not homogenous.

PROCAPREOLUS PYRENAICUS DEPERET, 1890

Deperet (1890) regarded "*C.* *pyrenaicus* (ca. 35 kg) from Early Pliocene of Roussillon (France) as a transitional evolutionary stage between *Pliocervus matheroni* and *Croizetoceros ramosus*. According to Heintz (1970) and Dong (1996), the antler morphology of "*C.* *pyrenaicus* is not related to *Croizetoceros ramosus* because of the essential difference in their antler bauplan. The antlers of "*C.* *pyrenaicus* are characterized by the high position of the first short ramification, which forms an acute angle with beam. The second tine is situated on the posterior side of the beam, unlike *Croizetoceros* (Deperet 1890: pl. VIII, fig. 3; Heintz 1970: 57, fig. 102; Dong 1996: pl. 2, fig. 3). The antler beam becomes somewhat flattened above the first ramification. P₄ shows a certain trend toward molarization (Dong 1996). According to Dong (1996) the antlers of "*C.* *pyrenaicus* show a certain resemblance with *Procapreolus* and I adjoin this opinion.

PROCAPREOLUS CUSANUS (CROIZET & JOBERT, 1828)

The remains of a small-sized deer from the Late Pliocene of Ravine Les Etouaires (=Perrier-Etouaires, = Boulades: Depéret 1884), France, were described under several species names. The species name *Cervus cusanus* appeared in the bibliographic notes of Croizet & Jobert's (1828) volume dedicated to fossil remains from the Department Puy-de-Dôme. This publication also contains a figure of the complete right antler with a frontal and part of parietal bones (Croizet & Jobert 1828: Pl. VIII, figs. 1-2). The second volume of Croizet & Jobert's work with description of the species was never published afterwards (Heintz 1970). The first description of *Cervus cusanus* Croizet & Jobert was published by Pomel (1853). Pomel (*ibidem*) also proposed definitions for new species *Cervus leptocerus*, *Cervus platycerus*, and *Cervus furcifer*. Those new species are characterized by the same size and the antler bauplan as in *C. cusanus*, differing in minor morphological details, which are regarded by Heintz (1970) as individual variants of the same species. Depéret (1884) proposed a new species name *Cervus neschersensis* for a smaller cervid from Ravine Les Etouaires characterized by more flattened antlers with comparatively lower position of the first tine. The measurements of a mandible ascribed by Depéret (1884) to *Cervus neschersensis* correspond to the measurements of the specimen PET809 from MNHN of Paris. Heintz (1970) demonstrated that all species described by Pomel (1853) and Depéret (1884) fall within the range of variation of *Procapreolus cusanus*. According to Heintz (1970), the collection that was studied by

Croizet & Jobert (1828) does not contain any antler that rigorously correspond to the original illustration. Possibly, the antler chosen by Heintz (1970) as a neotype (Fig. 3, B) is the specimen figured by Croizet & Jobert (1828).

Korotkevich (1970) included the species under discussion in the genus *Procapreolus*. Valli (2010) proved that *Procapreolus cusanus* is a telemetacarpal cervid, since it is characterized by a peculiar for the telemetacarpal deer shape of post-glenoid foramen, which is not completely surrounded by squamosal bone and bordered in its posteromedial part by petrous bone.

P. cusanus is the most advanced species of the genus that survived in Early Villafranchian of Western Europe. The geographic distribution of *P. cusanus* is quite restricted: the fossil remains that certainly belong to this species are reported from France, Italy, England (Heintz 1970; Abbazzi et al. 1995; Lister 1999). This is a rather small-sized species with the estimated body mass about 30 kg. Our knowledge about this species is still incomplete and the observed evolutionary specialization is reported only for its flattened antlers and its dentition, which lost the archaic *Palaeomeryx* fold and the basal structures (cingulum). The antlers of *P. cusanus* develop a flattened extension in their distal parts that attains the extreme expression at adult males (Heintz 1970). The beam segment between the first and the second ramifications is strongly flattened and represents a secure diagnostic characteristic from other species of *Procapreolus* that may eventually develop small flat extensions in the area of the ramifications, while their beam between the ramifications is always cylindrical. The position of the first tine is quite variable: the height of the first ramification varies from 63 to 145 mm (n=7). The length of the second segment is variable too, but seems to be comparatively longer than at other species of the genus (70 – 110 mm; n=4). Mature antlers of *P. cusanus* may bear up to five tines. This is an exceptional case among species of the genus *Procapreolus* characterized by the uniform three-tined antlers.

P_4 is always molarized: the metaconid is fused with the paraconid; the posterior wing of the metaconid may be weak or missing (Fig. 6). The premolar/molar ratio amounts to ca. 69% and corresponds to the general dental row proportions of the genus. Upper molars are supplemented with protoconal fold, hypoconal spur, while the true cingulum is never developed.

Cranial remains of *P. cusanus* are poorly known. The type specimen of Deperet's *Cervus buladensis* is the only known antlered braincase of this species that belongs to a young individual. The pedicles are relatively long (L>D), with circular cross-section, almost

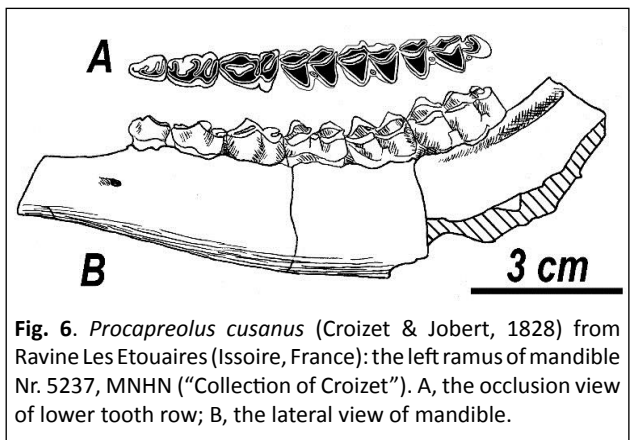


Fig. 6. *Procapreolus cusanus* (Croizet & Jobert, 1828) from Ravine Les Etouaires (Issoire, France): the left ramus of mandible Nr. 5237, MNHN ("Collection of Croizet"). A, the occlusion view of lower tooth row; B, the lateral view of mandible.

parallel to each other, and strongly sloped back from the face as on modern *Muntiacus*. The parietal bones are somewhat convex, the lambdoid suture is M-shaped. The bullae tympani are small and compressed. The frontal bones are relatively narrower with respect to the braincase breadth (frontal breadth to braincase breadth ratio attains 90.0%) if compared to the braincase from Gephyra, Greece (83.1%) described by Cregut-Bonnoure & Tsoukala (2017: fig. 7) as *Procapreolus cusanus*. Possibly, the relatively narrow frontal bones are correlated with young individual age of the specimen from Les Etouaires.

The relatively shortest pedicles of *P. cusanus* among the species of *Procapreolus* is another advanced evolutionary character of this species. However, *P. cusanus* maintains the plesiomorphic condition of the position and orientation of pedicles: the sloped backward parallel pedicles of the type specimen of *C. buladensis* remind the most primitive representatives of the so-called “crown deer” grouped in the subfamilies Cervinae and Capreolinae. The position of the pedicles on *P. cusanus* is more primitive than on *P. moldavicus* and *P. pentelici* from Gephyra, which are characterized by somewhat divergent pedicles. I cannot exclude that the parallel orientation of the pedicles in the braincase specimen of *P. cusanus* is an ontogenetic variation corresponding to its young individual age. However, it is necessary to mention that the male skull of *P. moldavicus* from Weze-1 also belongs to a young (prim adult) individual with thin antlers and short first tine as on the specimen under discussion *P. cusanus*. The space between pedicles in the skull from Les Etouaires is larger than in Modern *Capreolus*.

Table 1. Measurements of the antlered braincase of *Procapreolus cusanus* from the collection of MNHN (Paris) compared to *P. graecus* from Gephyra (Greece) (adapted from Cregut-Bonnoure & Tsoukala 2017), and modern *Mazama americana* (Nr. 4056, “La Specola”, Florence).

| Measurements | <i>P. cusanus</i> | <i>P. graecus</i> | <i>M. americana</i> |
|-------------------------------|-------------------|-------------------|---------------------|
| Frontal breadth | 64.0 | 75.6 | 38.0 |
| Breadth behind pedicles | 57.6 | 62.8 | 49.0 |
| Maximal breadth of braincase | 67.5 | | |
| Breadth of occiput | 72.4 | | 66.6 |
| Height of occiput | 48.2 | | 49.5 |
| Breadth of occipital condyles | 39.3 | | 43.8 |
| Length of pedicle (sin/dx) | 26.0 / 27.2 | | |
| DAP pedicle (sin/dx) | 19.2 / 18.8 | | |
| DAM pedicle (sin/dx) | 20.6 / 20.0 | | |
| DAP burr (sin/dx) | 36.5 / 31.0 | | |
| DLM burr (sin/dx) | 38.4 / 32.9 | | |
| DAP above burr (sin/dx) | 26.2 / 21.2 | | |
| DLM above burr (sin/dx) | 26.0 / 22.3 | | |
| L orbit – pedicle (sin) | 56.2 | | |

Genus *Capreolus* Frisch 1775

The modern genus *Capreolus* is a peculiar specialized small-sized dweller of the middle-latitude forests with specific adaptations to the seasonal climate with cold winters, such as the prolonged gestation (Geist 1998). This is a telemetacarpal deer, however its nasal cavity (at the posterior aperture of nares) is not divided completely by the vertical plate of vomer as in *Alces* (Brooke 1878). Although Flerov (1952) regards the roe deer *Capreolus capreolus* as a primitive cervid, which maintained some muntiacine traits, the cranial and dental morphology of *Capreolus* is very advanced. Pedicles are rather short, set in a more vertical position if compared to *Procapreolus*, with short space between them. Nasal bones are long and extended behind the line connecting the anterior edges of orbits (Fig. 5, C). The preorbital fossae are small, much smaller than in *Procapreolus*. Upper canines are lost as in *Alces*, thus representing the rare exception among modern Capreolinae that maintain upper canines during all their life. The protoconal fold in upper molars is lost; the *Palaeomeryx* fold is never present in modern species, however it is recorded in the earliest known species *Capreolus constantini* from Pliocene (MN16) of Udunga, Trans-Baikal Area (Vislobokova et al. 1995). P_4 is highly molarized. The premolar/molar ratio varies between 69.6% and 74.6% and indicates a generally longer premolar series than at *Procapreolus* (Vislobokova & Kalmykov 1994). Antlers maintain the three-pointed bauplan as in *Procapreolus*. Unlike *Procapreolus*, roe deer antlers are normally distinguished by the stronger development of burr and the specific pearling that covers the proximal part of the antler beam.

CAPREOLUS CUSANOIDES KÄHLKE, 2001

According to Kahlke (2001), *Capreolus cusanoides* from Untermassfeld (Germany, ca. 1.02 Ma) is the earliest roe deer in Western Eurasia. This is a small-sized deer (ca. 38 kg) similar in body size to modern European roe deer. Kahlke (2001) noticed the great similarity of antlers of the roe deer from Untermassfeld with *Procapreolus cusanus*, while the morphology of dentition of *Capreolus cusanoides*, according to Kahlke (2001), is similar to the modern roe deer. Nonetheless, the series of premolars in the only known complete mandible IQW 1993/24 360 from Untermassfeld is unusually long: the premolar/molar ratio amounts to 91.1%. Such a long premolar series approaches the roe deer from Untermassfeld to the most primitive Late Miocene forms of *Procapreolus*, *P. ucrainica*. The length of premolar series in *Procapreolus cusanus* from Perrier (France) is relatively shorter. It is difficult to give an evolutionary and morpho-functional interpretation for such an exceptionally long premolar series based on a single available specimen. Pedicles of *C. cusanoides* are short and robust, suggesting the advanced evolutionary specialization. It is important to mention that the antler morphology of *C. cusanoides* does not correspond to the typical for *Capreolus* antler shape, since the presence of large tubercles in the proximal part of antlers is an important diagnostic character of the genus (Flerov 1952; Lister et al. 1998). The oldest Pliocene roe deer *Capreolus constantini* is already characterized by the well-developed antler tubercles (Vislobokova et al. 1995). Therefore, *Capreolus cusanoides* seems to be rather a specialized capreoline that does not fit the evolutionary trend

within the genus *Capreolus*. However, definite conclusion on the systematic position of this species is not possible for the moment because of the scarcity of available remains.

CAPREOLUS SUESSENBORNENSIS KAHLKE, 1956

This is a somewhat larger form of the roe deer (40-45 kg) from the Middle Pleistocene (ca. 600 kyr BP) of Central and Western Europe (Lister et al. 1998; Stefaniak 2015). Three-pointed antlers are characterized by strong spike-like tubercles and flattened beam between ramifications (Kahlke 1969). The main morphological distinction of *C. suessenbornensis* from the modern roe deer consists in somewhat flattened antler beam, which is regarded by Lister et al. (1998) as a distinguishing character of a subspecific level. The lower part of the antler beam may coincide with the axis of the pedicle as on the specimen M/K 4.7.66 (SMNH) from Mosbach, or may deviate sideward immediately from the burr and form an angle of 65-70° as the specimens 32860/9 and 32860/5 (SMNH) from Mosbach.

The right fragment of the mandible 32860/3 (SMNH) is quite robust: the height of the mandible below M_1 and M_2 amounts to 21.1 mm and 23.2 mm respectively; the thickness of mandible below M_1 and M_2 amounts to 11.9 mm and 12.3 mm correspondingly. The measurements of the mandible from Mosbach are close to those of the modern *C. capreolus*, however, the body of the mandible is more robust: the ratio between mandible thickness to mandible height below M_1 attains 56.4% at the specimen in question, while in modern roe deer this index varies between 48.3-49.8% (n=3, Uch-Bash, Iron Age, Crimea). Lower molars (M_2 and M_3) of the right mandibular fragment 32860/10 (SMNH) from Mosbach do not show any trace of the *Palaeomeryx* fold.

Middle Pleistocene remains of the roe deer are known only from Western and Central Europe (Stefaniak 2015) and are conspicuously absent from the paleontological record of the Eastern Europe (Alekseeva 1977).

CAPREOLUS CAPREOLUS (LINNAEUS, 1758)

The modern European roe deer is characterized by a set of cranial characteristics, which may be regarded as advanced: the contact between nasal and premaxillary bones in most cases is lost, the naso-frontal suture is V-shaped as nasal bones are wedged between frontals, and the braincase is relatively shorter than at Asian *Capreolus pygargus*. It is difficult to estimate the significance and the degree of the evolutionary specialization of such specific characters of European roe deer as the shrunken and uninflated auditory bullae that distinguish this species from *C. pygargus* (Flerov 1952; Lister et al. 1998).

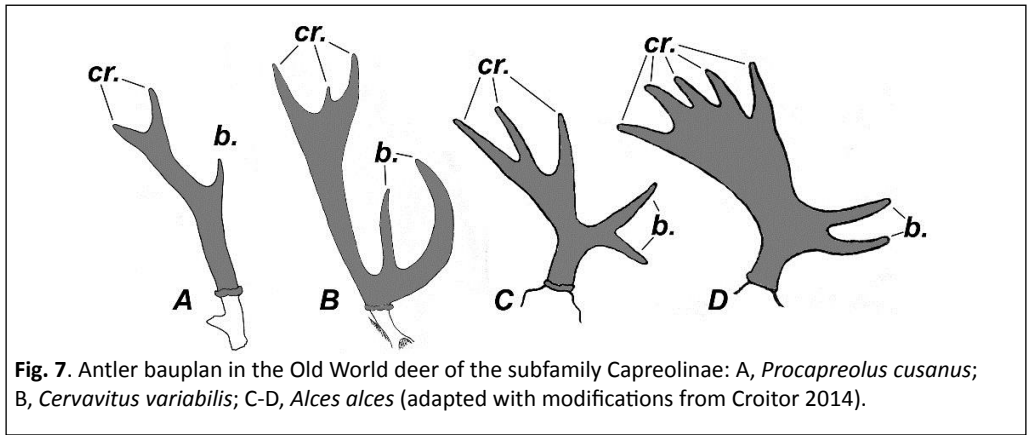
The close phylogenetical and systematical relationship between the modern *Capreolus* and its assumed Mio-Pliocene forerunner *Procapreolus* was accepted by many authors

(Czyżewska 1968; Korotkevich 1970; Vislobokova 1990; Vislobokova & Kalmykov 1994; Grubb 2000; Kahlke 2001; Di Stefano & Petronio 2002). This viewpoint is grounded on the obvious fact that *Capreolus* and *Procapreolus* share the basic antler bauplan characteristic of all *Capreolinae*. This basic capreoline antler construction (the high position of the anterior tine and the distal fork with the stronger anterior tine) can be seen also on modern *Ozotoceros* and *Alces*, as well as on the extinct *Cervavitus* and *Eocoileus*. Our knowledge on cranial morphology of most of fossil forms is insufficient for confirmation or rejection of the hypothesis on direct phyletic relationship between *Capreolus* and *Procapreolus*. Nonetheless, the western forms of *Procapreolus* most probably represent an extinct side lineage that did not live descendants. The best known *Procapreolus moldavicus* is a primitive form characterized by the plesiomorphic mixture of muntiacine, odocoileine, and roe deer cranial and dental characters, and some of them, like broad frontals and divergent pedicles, rule out the direct phyletic relationship between *Procapreolus moldavicus* and *Capreolus*. The parallel orientation of closely set pedicles in *Capreolus capreolus* reminds the archaic capreoline genus *Pliocervus*. However, *Pliocervus matheroni* and its Asian counterpart *Pavlodaria orlovi* are characterized by the quite specialized four-pointed antlers with an irregular section of the beam. Apparently, we are dealing with a broad and paleontologically still poorly known phylogenetic radiation of the capreolines characterized by mosaic combinations of shared characters that exclude the possibility of direct phyletic relationships between them.

Genus *Alces* Gray 1821

Elks represent a morphologically well outlined group of few easily recognizable cervid forms. *Alces* is characterized by the most advanced degree of premolar molarization and the specific cranial and antler apomorphies as the directed sideward pedicles, the horizontally oriented more or less long antler beams and the frequently developed distal palmation of antlers. The elk taxonomy is still debated. Azzaroli (1952) established a new genus *Libralces* with type species *Libralces gallicus* from Villafranchian fauna of Sènèze distinguished by the quite primitive cranial and dental characters: the long nasal bones articulated with premaxillars and the *Palaeomeryx* fold in the lower molars. Later, Azzaroli (1985) proposed to regard *Libralces* as a subgenus of the North American genus *Cervalces* Skott, 1885, which is characterized by the similar shape of muzzle. Vislobokova (1986, 1990) and Boeskorov (2001) recognize three valid genera of elks: *Libralces* Azzaroli 1952 with the type species *Libralces gallicus* Azzaroli, 1952; *Cervalces* Scott, 1885 with the type species *Cervalces scotti* (Lydekker, 1898), and the modern genus *Alces*. Vislobokova (1990) also considered the poorly known genera *Tamanalces* Verestchagin, 1957 and *Pseudalces* Flerov, 1962 from the South of European Russia as true elks. Breda (2001) and Stefaniak (2007) included all fossil elks in the genus *Cervalces*. This taxonomical solution is accepted by Nikolsky (2010), who divides *Cervalces* into three subgenera: *Libralces*, *Cervalces*, and *Latifrons*. According to Nikolsky (2010), *Cervus latifrons* Johnson, 1874 is the type species of the subgenus *Cervalces*. Kahlke (1969), Heintz & Poplin (1980), Lister (1987), and Brugal & Croitor (2007) included all elk species in *Alces*. In defense of the latter point of view, I can point

to the fact that all recorded characters distinguishing fossil and modern forms of elks concern only exosomatic organs (muzzle shape and details of antler morphology) and body size, i. e. the characters that are used to distinguish species within a genus.



The elk is a telemetacarpal cervid, however its nasal cavity (at the posterior aperture of nares) is not divided completely by the vertical plate of vomer. This specific character approach *Alces* to *Capreolus* and *Hydropotes* and distinguish from American telemetacarpal cervids (Brooke 1878). Lower premolars P_3 and P_4 are highly molarized: P_4 is functionally molariform, while P_3 represents the advanced degree of molarization with complete fusion of metaconid and paraconid. The lower molar series is relatively long: the premolar to molar series length ratio varies between 67.0 and 74.3% in the sample of the modern *Alces alces* stored in the NHML, and the premolar/molar ratios of all known complete lower tooth rows of fossil elks (*Alces gallicus* and *Alces latifrons*) fall within this range of variation. The general bauplan of unpalmed elk antlers reminds the basic antler type of Capreolinae (Fig. 7). The general antler construction in *Alces* is characterized by the development of main 3-5 tines: the first (basal) tine is directed toward the anterior, often is double or bifurcated (as in *Cervavitus variabilis*); the antler beam is bent toward the posterior in the area of the first bifurcation and in the simplest case is terminated by a fork (as in *Capreolus* and *Procapreolus*), but supernumerary tines are often present on the anterior side of the beam (if the antler is oriented in the vertical plane). The evolutionary modifications of the antler morphology in *Alces* concern only the number of supernumerary points that typically merge in a terminal antler palmation, and the length of basal segment of the antler (between the burr and the first/basal ramification).

ALCES GALLICUS (AZZAROLI, 1952)

The species was described from the Early Pleistocene lacustrine “maar” deposit dated back to 2.0-1.6 Ma (Breda 2001). Azzaroli (1952: 134, fig. 1) designated the heavily damaged and partially reconstructed articulated skeleton Nr. 96134 (PMUL) as a holotype of *Libralces gallicus*. Breda (2001) doubted that the antlered skull and postcranial mounted skeleton belongs to the same individual and excluded the

mounted postcranial bones from the holotype. According to Breda (2001), the better preserved articulated bones of a somewhat larger individual from the same locality chosen by Azzaroli (1952) as cotype, in fact belong to the same individual together with the antlered skull and therefore those postcranial bones are proposed to be considered as parts of the holotype of *Libralces gallicus*. *Libralces minor* Azzaroli, 1953 is a junior synonym of *Alces gallicus* (Azzaroli, 1952).

The estimated body mass based in the holotype skull from S n ze and the skull fragment from East Runton (M6101, NHML) amounts to ca. 400 kg. The skull of *Alces gallicus* is characterized by the specific for elks horizontal sideward direction of pedicles and is distinguished from modern *A. alces* by the low and broad braincase (Azzaroli 1952; Breda 2001) and the obtuse angle between occipital and parietal surfaces. The nasal bones are rather long and articulated with the praemaxillae. The orbital part of the type skull is destroyed and reconstructed with plaster, therefore the condylobasal length could not be measured. Other cranial measurements are indicated in the Table 2. The distance bregma – opisthocranium is shorter than the breadth of the neurocranium behind pedicles in the skull M6101 from East Runton. The breadth of the braincase attains 51.2% of the breadth of frontals. The angle between horizontal ramus of the mandible and its ascending part is 110  (Azzaroli 1953: 28, fig. 10A).

The extremely long basal segment of the antler between the burr and the distal palmation is a striking morphological feature of *Alces gallicus*. The antler beam is set along the pedicle axis; the position of the burr is oblique with respect to the beam axis (Breda 2001). The antler beams of the type specimen are gently curved and terminated with fan-shaped palmations supplemented with cone-shaped tines (only two terminal tines are preserved on the left antler). The antler beam is much longer than the palmated part of the antler. The total span of antlers could attain 2.20 m (Azzaroli 1952).

The upper molars (at list M³) are characterized by the presence of a large protoconal fold, while the hypoconal spur is absent. Upper molars are supplemented with large entostyle and weak lingual cingulum (Breda 2001). The lower molars are with strong ectostylids. According to Azzaroli (1952), the lower molars of the mandible from Weybourn Crag ascribed to *Alces gallicus* are characterized by the presence of a weak *Palaeomeryx* fold. *Alces gallicus* from S n ze. Heintz & Poplin (1980) and Breda (2001) disproved the fact of presence of the *Palaeomeryx* fold trace in *Alces gallicus*, since it is not seen in the holotype from S n ze. Apparently, Azzaroli (1952) was misunderstood, since he was referring to the specimen from Weybourn Crag, not to the type specimen from S n ze. My study permits me to confirm that the weak *Palaeomeryx* fold is present in M₁ and M₂ of the specimen M6227 (the holotype of *Libralces minor*). Nikolsky & Titov (2002) also reported the weak *Palaeomeryx* fold in lower molars of *Alces gallicus* from Liventsovka (Russia). Therefore, the occasional presence of a vestigial *Palaeomeryx* fold should be regarded as a specific character of *Alces gallicus*. Azzaroli (1952, 1953) assumed the possible presence of upper canines in *Alces gallicus*, but this presumption was not confirmed by other authors (Heintz & Poplin 1980; Breda 2001).

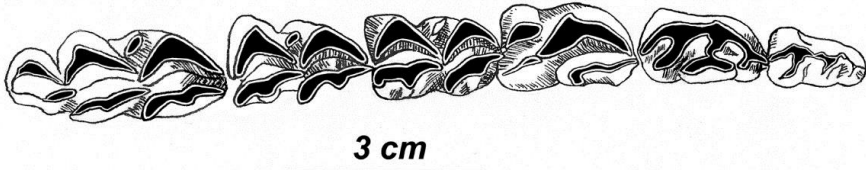


Fig. 8. The occlusal view of left lower cheek tooth row M6227 of *Alces gallicus* (Azzaroli, 1952) from the Cromer Forest-Bed Formation, exact locality is unknown (holotype of *Libralces minor* Azzaroli, 1953). Note the incomplete molarization of P_3 : its metaconid and paraconid are not fused.

Unlike geologically younger elks, P_3 in *A. gallicus* is not fully molarized: the metaconid and the paraconid in P_3 of the specimens M6227 and M6206 are not fused (Azzaroli 1953: fig. 4) and represent a distinguishing primitive character of this species (Fig. 8). It is difficult to make a reliable comparison with the holotype from S n ze, which is characterized by a complete fusion between the metaconid and the paraconid (Azzaroli 1952: fig. 2a), but the wearing stage of its dentition is much more advanced. It is important to mention that the similarly unmolarized P_3 with the open anterior valley is also characteristic to *Cervalces scotti* Lydekker from the Holocene of North America (Hibbard 1840: pl. II, fig. 1). Remains of *Alces gallicus* are known from France, England, Romania, Azov Area of Russia, Tajikistan (Azzaroli 1952, 1953; Heintz & Poplin 1980; Vislobokova 1986; Boeskorov 2001; Nikolsky & Titov 2002; Breda & Marchetti 2005; Radulesco 2005).

ALCES CARNUTORUM (LAUGEL, 1862)

The species is described from the final Early Pleistocene of Saint-Prest (France). According to Heintz & Poplin (1980), the intermediate body size that place the cervid in question between *Alces gallicus* and *Alces latifrons* is the main diagnostic character of this species. The fragment of the left maxilla SPR-70 (MNHN) with M^1 and M^2 is the lectotype of *Alces carnutorum* chosen by Heintz & Poplin (1980). Molars are low-crowned with the strongly sloped lingual wall (angle between labial and lingual walls of molars amount to 50°). The posterior wing of protocone is supplemented by a protoconal fold; the protoconal fold and the posterior wing of the protocone in both M^1 and M^2 have a tendency to close the small enamel isle between them. The hypoconal spur is not present in M^1 , but is well-developed and folded in M^2 . The entostyle is well developed and is particularly large in M^2 . The length of the M^1 crown attains 27.1 mm, the maximal breadth at the crown base attains 28.3 mm; the analogous measurements of M^2 are 30.3 mm and 29.0 mm.

Stefaniak (2007) ascribed to *Alces carnutorum* quite poor remains (isolated teeth, fragments of mandible and limb bones) from the Biharian deposits of Zabia Cave. The isolated incisives (I_1 and I_2) are characterized by symmetric chisel-like crowns as in modern *Alces alces*. The isolated P_3 (Stefaniak 2007: fig. 1B) shows the incomplete molarization as at *Alces gallicus* from Cromer Forest-Bed formation. Upper molars from Zabia Cave ($L M^1 = 25.3\text{--}25.9$ mm, $n=2$; $L M^2 = 27.6\text{--}28.8$ mm, $n=2$) are slightly smaller than the lectotype from Saint-Prest. The fragment of the mandible from Zabia Cave

shows a more acute angle (96°) between the mandibular body and its ascending part if compared to the modern elk (110°) (Stefaniak 2007). Apparently, the acute angle between the horizontal and ascending parts of the mandible is correlated with a comparatively shorter orbitofrontal part of the skull in the elk from Zabia Cave. The presence of the *Paleomeryx* fold is not reported (Stefaniak 2007).

Table 2. Cranial measurements of *Alces gallicus* and *Alces latifrons*; (*), right; (**), left.

| Measurements | <i>A. gallicus</i> , holotype (Nr. 96134, PMUL) | <i>A. gallicus</i> , East Runton (M6101, NHML) | <i>A. latifrons</i> , Mundesley (M6553, NHML, holotype of <i>Libralces gallicus</i>) |
|--|---|--|---|
| Frontal breadth | | ca. 216.8 | ca. 281.4 |
| Length of upper tooth row (P ² -M ³) | 129.0 | | |
| Braincase breadth behind pedicles | | 111.0 | 129.5 |
| Distance bregma – opisthocranium | | 105.8 | 151.5 |
| Occipital height (basion – opisthocranium) | 115.2 | 111.4 | 144.4 |
| Occipital breadth | 168.6 | 162.7 | 250.0 |
| Breadth of occipital condyles | 83.9 | 85.3 | 131.1 |
| Distance P ² – prosthion | ca. 163.0 | | |
| Total length of right antler | 1160.+ (*) | | |
| Dorsoventral diameter of pedicle | 62.6 (*) | 63.2 (**) | 95.5 (**) |
| Anteroposterior diameter of pedicle | 70.5 (*) | 75.1 (**) | 113.9 (**) |
| Circumference of pedicle | 230.0 (*) | 230.0 (**) | 345.0 (**) |
| Dorsoventral diameter of antler above burr | 65.6 (*) | 59.0 (**) | 95.3 (**) |
| Anteroposterior diameter of antler above burr | 66.4 (*) | 67.6 (**) | 101.4 (**) |
| Circumference of antler base | 209.0 (*) | 200.0 (**) | 320.0 (**) |

The pedicle of *Alces carnutorum* is robust and directed sideward, somewhat compressed dorsoventrally as at *Alces gallicus*: its dorsoventral diameter amounts to 55 mm, while the anteroposterior diameter attains 60 mm (Heintz & Poplin 1980). The postorbital (=frontal) breadth based on the badly preserved left frontal bone (210 mm) is just slightly below the measurements provided by the elk sample from Mosbach (220-230 mm; Heintz & Poplin 1980) and *A. gallicus* from East Runton (Tab. 2). Heintz & Poplin (1980), taking in account the fragmentary and incomplete fossil material from Saint-Prest, do not exclude the subspecific status or synonymy of *Alces carnutorum* with *Alces gallicus* or *Alces latifrons*. The species is reported from France, Germany, Northern Italy, Romania and Poland (Heintz & Poplin 1980; Kahlke 1997; Radulesco 2005; Stefaniak 2007).

ALCES SP. FROM MOSBACH

The case of the remains from Mosbach (Germany) reveals the imperfect taxonomical model of fossil elks and the insufficient knowledge of their morphology and intraspecific variation. Remains of elks from Mosbach are abundant, but they cannot be attributed to any of the recognized fossil species of *Alces* because of their unknown exact stratigraphic provenance. There are two levels present at Mosbach. One is comparable in age to other European sites with *Alces latifrons* and the other to European sites with *Alces carnutorum* (Breda & Marchetti 2005). The impossibility to assign the material from Mosbach to any of these species reveals our poor understanding of morphological distinction between the above mentioned species.

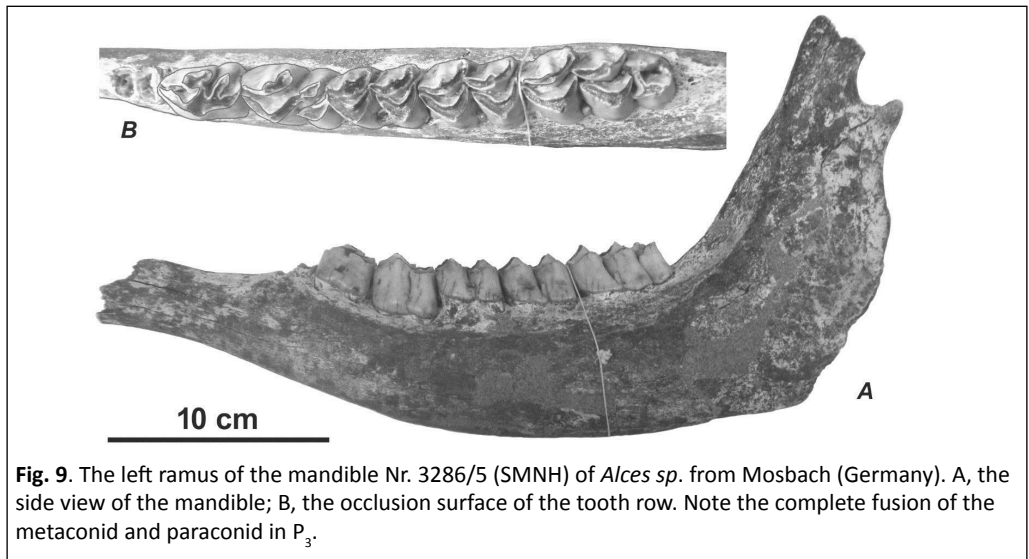


Fig. 9. The left ramus of the mandible Nr. 3286/5 (SMNH) of *Alces* sp. from Mosbach (Germany). A, the side view of the mandible; B, the occlusion surface of the tooth row. Note the complete fusion of the metaconid and paraconid in P₃.

The left hemimandible 3286/5 (SMNH) is characterized by the presence of a weak trace of the *Palaeomeryx* fold in M₁ and M₂. M₃ is also supplemented with an enamel fold that reminds the *Palaeomeryx* fold. P₄ is molariform; P₃ is molarized: its metaconid and paraconid are fused and close the anterior valley from the lingual side. The advanced molarization of P₃ distinguishes the elk from Mosbach from the samples described

as *A. gallicus* and *A. carnutorum*. The angle between the body of the lower mandible and its ascending part amounts to 130° and exceeds significantly the value reported for *A. carnutorum* from Zabia Cave. The fragment of right hemimandible 32861/33(SMNH) from Mosbach with M₂ also shows a clear rudiment of the *Palaeomeryx* fold (Fig. 10).

The maxilla Nr. 32861/8 with M² and M³ (L M² = 33.0 mm; D M² = 31.0 mm; L. M³ = 31.1 mm; D M³ = 30.0 mm) is somewhat larger than the lectotype of *Alces carnutorum*. The styles of both molars are strong and protruding; the protoconal fold is present and tends together with the posterior wing of M² to isolate a small enamel isle as in *A. carnutorum*. The spur of the hypocone is absent in M² and well-developed in M³. The entostylid is vestigial in M² and better developed in M³, but much smaller if compared to the lectotype of *A. carnutorum*. The elk from Mosbach is characterized by a set of the advanced characteristics such as the absent lingual cingulum and the reduced entostylids, the molarized P₃, the larger angle between the mandibular body and the ascending ramus of mandible, which are combined with the comparatively small size and the vestigial *Palaeomeryx* fold.

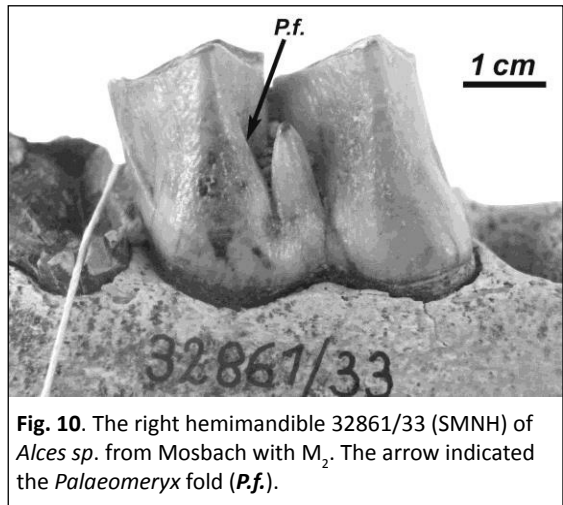


Fig. 10. The right hemimandible 32861/33 (SMNH) of *Alces* sp. from Mosbach with M₂. The arrow indicated the *Palaeomeryx* fold (*P.f.*).

ALCES LATIFRONS (JOHNSON, 1874)

The holotype of species is a left antler with a part of frontal bone from Hasbro (= Happsburgh: Azzaroli 1953), Forest-Bed, Norfolk (Johnson 1874). This is one of the largest fossil cervid species of Western Palearctic with body mass attaining 870 kg (the body mass estimation is based on the skull M6553 from Mundesley, NHML). The skull M6553 is characterized by the elongated proportions of the neurocranium if compared to *A. gallicus*: the distance bregma – opisthocranium measured in the skull from Mundesley is significantly longer than the braincase breadth measured behind pedicles. The relatively long braincase is regarded as a primitive character in cervids (Vislobokova 1990) and in the neurocranium of *A. latifrons* from Mundesley apparently is more primitive than that of *A. gallicus*, which was considered by many authors as a primitive forerunner of *A. latifrons*. The braincase from Mundesley is also relatively narrow with respect to the frontal bones and attains 46% of the frontal breadth.

The maximal span of antlers attained 2.5 m (Azzaroli 1953). The distal palmation is fan-shaped with long radially oriented tines. The length of the cylindrical beam and the length of the palmated part of antler roughly represent a proportion 40:60 (Kahlke 1969: tab. XXVIII). The antler burr is perpendicular with respect to the longitudinal axis of pedicle and beam.

The metaconid and the paraconid of P^3 are fused at the specimen from Mundesley (Azzaroli 1953: fig. 11) and in the lower mandibles from Süßenborn (Kahlke 1969: figs. 4, 5). Some isolated upper molars from Süßenborn are characterized by the presence of a weak lingual cingulum as in *A. gallicus* (Kahlke 1969: fig. 3). The protoconal fold is weak, especially in molars on the advanced stage of wear. In some molars, the posterior wing of the protocone include a small enamel isle that resulted from the fusion of the protoconal fold with the posterior wing of the protocone (Kahlke 1969: fig. 3).

ALCES ALCES (LINNAEUS, 1758)

The oldest elks of modern type in Europe were reported from the lower Paleolithic dated to the border between Middle and Upper Pleistocene (Stefaniak 2007) or, according to Kurten (1968), from Riss Glaciation (200-100 ky BP). Some authors (Vörös 1985; Breda & Marchetti 2005; Stefaniak 2007) regard "*Alces brevirostris* Kretzoi" from the Quaternary deposits of Solymar-Ördöglyuk Cave (Hungary) as a transitional form between *Alces latifrons* and *Alces alces*. Reportedly, this elk form is characterized by the longer nasal bones articulated with premaxillary bones and the relatively long antler beam. It is necessary to clarify that the species name "*Alces brevirostris*" is not valid, since the manuscript of Kretzoi with species description was never published and the original cranial material studied by Kretzoi subsequently was lost (Vörös 1985). Only a brief description of the postcranial articulated skeleton and a figure of a shed antler were published by Vörös (1985), but the diagnosis of the species was not provided.

The modern forms of *Alces alces* show a certain range of variation in the body size, antler shape, and cranial morphology. Some bulls of *Alces alces* from Sweden (the type locality) may reach 686-713 kg of body weight, while the body mass of smaller Manchurian bulls rarely exceed 300 kg (Geist 1988). The cranial shape of modern elks is very peculiar in its apomorphic characters: the skull is greatly lengthened in the premaxillary region, the extremely long praemaxillae lost contact with nasals in all modern forms, the nasal bones are short, the nasal aperture is sizable, and the vomer does not divide the aperture of the posterior nares (Franzmann 1981; Breda & Marchetti 2005). However, the nasopremaxillary contact was maintained in the Caucasian subspecies *Alces alces caucasicus* Verestchagin, 1955 (now extinct). The angle between parietal and occipital surfaces of the braincase is acute. Upper canines are absent at both sexes. Upper molars are supplemented with protoconal fold, which still can be seen in the M^3 of the modern *Alces alces* (Lydekker 1915: p. 231, fig. 35). According to Nikolsky & Boeskorov (2011), the European elk shows higher frequency of advanced morphological variants of P_3 (disjunction between protoconid and metaconid and between protoconid and hypoconid) than East Siberian forms.

The shape and development of antler palmation is not constant and varies within the species, as well as within the same population of elks. The antlers are typically unpalmed in the subspecies *Alces alces caucasicus* and *Alces alces cameloides* Milne-Edwards, 1867 (= *Alces americanus cameloides* fide Boeskorov 2001), but the underdeveloped palmation is also recorded in other subspecies as individual variants. The unpalmed elk antlers represent a typical tree-pointed capreoline bauplan (Fig.

7, C). The degree of development of palmation in elks depends on the individual age, the quality of nutrition, and the physical state of animal (Flerov 1952). The antler beam is cylinder-shaped and short, much shorter than the breadth of the cup-shaped palmated portion of the antler. Apparently, the antlers of the modern *Alces alces* are less specialized among the elk species and stand closer to the initial capreoline antler type. The area of distribution of *Alces alces* includes the circumpolar boreal forests of Eurasia and Northern America (Flerov 1952; Franzmann 1981; Boeskorov 2001).

The phylogenetic lineage of elks in Western Eurasia is traced in the paleontological record only from Early Pleistocene (Heintz & Poplin 1980; Breda & Marchetti 2005). The views on phylogenetic relationships and evolution of elks did not provoke controversies and debates. Azzaroli (1953), Heintz & Poplin (1980), Lister (1987), Breda & Marchetti (2005), and Nikolsky (2010) regard Eurasian fossil elks as chronospecies of a single phyletic lineage characterized by the gradual increase of the body size and the shortening of antler beam. However, the phylogenetic model of Eurasian elks could be more complicated. Certainly, the northern part of the Asian continent was the core area of the elk evolution and dispersals. The most ancient and quite poor fossil remains of a cervid form showing the typical elk shape of frontal bone with the sideward orientation of the pedicle is reported from Pliocene of Udunga, Trans-Baikal Area (Vislobokova et al. 1995). The elk from Udunga is characterized by an oblique position of the antler burr as in *Alces gallicus* and a slight anteroposterior compression of the pedicle. The oldest remains of *Alces gallicus* are known from the Middle Villafranchian of Navrukho (Tajikistan) and Livenzovka (Azov Sea Area of Russia) (Vislobokova 1986; Nikolsky & Titov 2002). The antlers of *Alces gallicus* seem to be extremely specialized and most distant from the initial capreoline antler bauplan. Some characters (*Palaeomeryx* fold, unmolarized P_3 , long nasal bones) are still primitive, however the relatively short braincase suggests that we are dealing with a quite advanced elk form that most probably represents a side evolutionary branch that dispersed until Western Europe. The unmolarised P_3 of *Cervalces scotti* may be regarded as an evidence that this North American species together with *Alces gallicus* take part from the first successful evolutionary radiation of elks, i. e. before the process of the P_3 molarization that occurred in *Alces latifrons*. The elongated braincase of *Alces latifrons* rules out the direct phyletic relationship with European *Alces gallicus*. One can assume that *Alces latifrons* evolved in Asia and then substituted *Alces gallicus* during the early Middle Pleistocene. The high frequency of primitive morphological type in modern Asian elks reported by Nikolsky & Boeskorov (2011) also may be regarded as an argument for the origin of *Alces alces* in the Asian part of its actual area of distribution and its subsequent dispersal to the western part of Eurasia.

The question on the origin of elks remained unresolved for a long time mostly because the extreme cranial and dental specialization of this group does not allow to trace the morphological affinity with other cervid groups. Flerov (1952: 13) regarded *Eucladoceros* as a possible forerunner of *Alces*, but this viewpoint was not supported. Dental and postcranial remains from the Pontian of Moldova described as *Alces maeoticus* Pavlow, 1926 actually belong to a giraffid *Palaeotragus* (Heintz & Poplin

1980). Vislobokova (1986) regards *Pseudalces mirandus* Flerov, 1962 from the mixed fauna of Villafranchian type of Kosiakinskiy Quarry as a side branch of elk radiation, however, the single known cranial fragment of this deer with P^4 - M^3 is characterized by the rather small compressed mesiodistally P^4 as in Cervinae, while in *Alces* (and all Capreolinae) P^4 is broad and relatively large. Therefore, *Pseudalces mirandus* is a deer of the subfamily Cervinae and most probably is close to or even synonymous with the giant *Arvernoceros verestchagini* David, 1992 (Croitor 2005, 2009). *Tamanalces caucasicus* Vereshchagin, 1957 from Quaternary fauna of Tamani is another poorly known deer considered by Vislobokova (1986) as an elk. This species is based on a poor fragment of a frontal bone with the pedicle and basal part of the antler. Taking into account other antler remains yielded by the site of Tamani, *Tamanalces caucasicus* most probably is a junior synonym of *Praemegaceros solilhacus* (Croitor 2006b).

The hypothetic forerunner of the genus *Alces* should be sought in the Late Miocene of middle latitudes of Eurasia. *Cervavitus variabilis* from the Late Miocene of Eastern Europe represents a special interest as a possible ancestral form of elks (Fig. 7). This medium-sized deer was traditionally regarded as a transitional evolutionary stage between the Muntiacinae and the Cervinae (Khomenko 1913; Flerov 1952; Czyzewska 1968; Korotkevich 1970; Vislobokova 1980). It is necessary to mention that Czyzewska (1968) and Korotkevich (1970) did not find essential differential diagnostic characters of cranial and dental morphology between *Cervavitus* from *Procapreolus*. It is also important to keep in mind that the holometacarpal condition of forelimbs for *Cervavitus* from Eastern Europe was never demonstrated. In my opinion, *Cervavitus variabilis* belongs to the Late Miocene radiation of *Capreolinae* together with *Pliocervus*, *Pavlodaria* and *Procapreolus* (Croitor 2014). *Cervavitus variabilis* is characterized by the enlarged premolar teeth and the tendency of molarization of P_4 , the well-developed *Palaeomeryx* fold in the lower molars and the protoconal fold in the upper molars, the short compressed dorsoventrally pedicles and the flattened antlers showing the characteristic for the Capreolinae three-pointed bauplan and could be closely related to the Late Miocene forerunner of *Alces* (Croitor 2014). Here should be mentioned the shed antler from sandy-gravel deposits near Mariupol (Ukraine) described by Pidoplichko and Flerov (1952) as *Cervus (Cervodama) pontoborealis* and assumed to be a Pliocene fallow deer related to the modern *Dama mesopotamica*. Korotkevich (1970) and Vislobokova (1990) noted that the antler from Mariupol is similar to the palmated antlers of *Alces alces*. The antler from Mariupol is quite small (the diameter of the beam amounts to 35 mm), however its resemblance to the antler shape of the modern *Alces alces* is striking: the antler base is circular, the beam is short ($L = 40$ mm) and the distal part of the antler form a fan-shaped palmation with six radial tines. The diameter of the antler base is slightly inferior to the measurements of the Pliocene elk from Udunga (43.0×40.3 mm; 59.3×65.0 mm) reported by Vislobokova et al. (1995). The maximum length of the antler attains 60 cm (Pidoplichko & Flerov 1952). One can assume that the antler from Mariupol belongs to a small-sized ancient form of elk.

Genus *Rangifer* H. Smith, 1827*RANGIFER TARANDUS* (LINNAEUS, 1758)

The genus *Rangifer* is characterized by the advanced shape of the braincase (short and broad), the presence of small upper canines, and the large complicated and very variable in shape antlers, which are present at both sexes. Typically, the reindeer antlers bear two anterior tines inserted in the proximal part of the beam, a specific posterior tine in the middle part of beam, and multiple posterior crown tines that often form a small palmation. The nasal cavity of reindeer (at the posterior aperture of nares) is completely divided by the vertical plate of the vomer (Vislobokova 1990). The earliest presence of reindeer in Europe is reported from the early Middle Pleistocene of Germany, France, and England (van Kolfschoten et al. 2011); however, only German reindeer fossils from Mosbach and Süßenborn were a subject of systematic and taxonomical study (Kahlke 1963, 1969). The antlered reindeer braincase from the Middle Pleistocene of Mosbach sands is characterized by a very low position of the first (= ice) tine and the second (= ocular) tine and a simple branched distal crown. Kahlke (1963) described the reindeer from Mosbach and Süßenborn as a new subspecies *Rangifer arcticus stadelmanni* (= *R. tarandus stadelmanni* Kahlke, 1963 *vide* Croitor 2010; van Kolfschoten et al. 2011) and assumed its close relationship with the barren-ground caribou of North America.

The taxonomy of the Late Pleistocene reindeer from Western Eurasia still requires a careful and detailed study. Here I will indicate only the essential taxonomic issues. Several names for fossil reindeer were proposed in old scientific publications. However, the name bearing specimens, including the fine cranial material, remained practically unstudied.

Desmarest (1820) described a new species *Cervus guettardi* based on Cuvier's (1823) brief description fossil reindeer antlers from Etampes. The name "*Rangifer guettardi*" Desmarest, 1820 (*sic*) was applied by Bouchud (1967) for reindeer remains from the grotto near Foix (France) dated back to 7 100 years BC. The comparatively large size of the reindeer from Foix is close to the fine complete reindeer skeleton from Villestoft (Denemark) dated back to 11 000 years BC (Bouchud 1966). Lydekker (1886) regarded *Cervus guettardi* Desmarest as a junior synonym of *Rangifer tarandus* Linnaeus. I adjoin this viewpoint, since the antler remains used for description of *Cervus guettardi* belong to young individuals and do not provide any particular diagnostic character that distinguish this form of the reindeer.

Owen (1846) described a new species *Cervus bucklandi* based on a basal fragment of a shed antler from the cave of Kirkdale. According to Owen (*ibidem*), the antler from Kirkdale is very close to *Cervus guettardi*, but somewhat larger. Therefore, *Cervus bucklandi* Owen, 1846 is another junior synonym of *Rangifer tarandus*. Owen (1846) also reported a fine antlered skull of a reindeer (*Cervus tarandus*) from Bilney Moor near East Dereham, England. The antlers are rather thin and cylinder-shaped (Owen 1846: fig. 197), which remind *Rangifer tarandus tarandus* and *R. tarandus stadelmanni* from Mosbach. The reindeer from Bilney Moor represents a rather small-sized form, however, only its breadth at pedicles (76.2 mm) is reported.

Rutten (1909) based his extinct subspecies *R. tarandus diluvii* on fossil remains stored in the Zoological museums from Utrecht and Leiden (the Netherlands). The asymmetric underdeveloped or missing subbasal antler tine ("Ocularspröss" according to Rutten 1909: 71) is the main distinguishing character of Rutten's taxon. Therefore, *R. tarandus diluvii* Rutten, 1909 reminds *Cervus bucklandi* Owen, 1846. Actually, the asymmetric and underdeveloped subbasal tine is common at the reindeer and *R. tarandus diluvii* Rutten, 1909, most probably, is just another synonym of *Rangifer tarandus* Linnaeus.

Scharff et al. (1917: 63) established another subspecies of extinct reindeer *R. tarandus hibernicus* based on a quite complete antlered skull from the Ashbourne bog (figured in Carte 1864) and fragmented osteological material from Castlepook Cave (Ireland). Following the diagnostic characters for the modern reindeer proposed by Lönnberg (1909), Scharff et al. (1917) provided only the measurements and the morphological description of the nasal bones of the Ashbourne skull. The nasal bones are flat, as at the Swedish *Rangifer tarandus tarandus*; the width of the nasal cavity is relatively large, the nasal bone breadth and length amount to 16 mm and 131 mm respectively. The antlers of the Ashbourne skull are large and richly branched, their main beam and basal tines are terminated with broad palmations reminding the reindeer from Villestofofte. According to Bouchud (1966), the age of the Ashbourne skull is dated back to the Allerod oscillation (10 000 years BC).

Flerov (1934) described a fossil reindeer from the Late Paleolithic ("Solutrean age" *vide* Flerov 1934; ca. 16 000 years BC *vide* Bouchud, 1967) site of Malta (Irkutsk, Siberia) as *Rangifer constantini*. This is the best defined fossil subspecies of the reindeer characterized by the narrow and high muzzle (the ratio between the cranial breadth at P² to the rostral height at rhyinion is 57.9%), the elongated head, and the relatively large teeth (larger than at any other modern and fossil reindeer form). The relatively large size of the upper cheek teeth is the most remarkable characteristic of this reindeer: the length of M¹-M³ series amounts to 56.5 mm. The nasal bone length (116.7 mm)

is shorter than at *R. tarandus hibernicus*, but longer than at the reindeer from Foix and Villestofofte (Bouchud 1967). Bouchud (1966) regarded *Rangifer constantini* as a forest reindeer. However, the comparatively small body size of the reindeer from Malta, its relatively short limb bones, simple long antlers with small palmations (Fig. 11, C), and large cheek-teeth define *R. tarandus constantini* as rather an open-landscape grazing form (Croitor 2010). The remains of large-

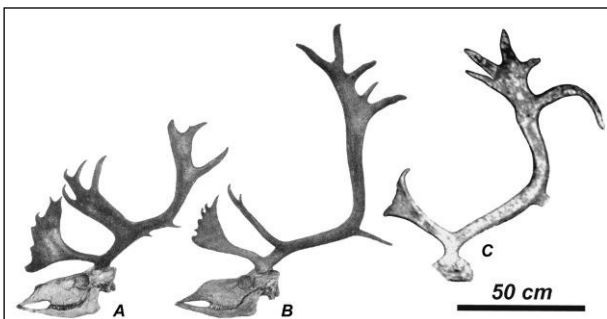


Fig. 11. Antler shape in reindeer: A, the modern woodland reindeer *Rangifer tarandus terranovae* Bangs, 1896 (adapted from Allen 1900); B, the modern barren ground reindeer *Rangifer tarandus groenlandicus* (Borowski, 1780) (adapted from Allen 1900); C, the tundra-steppe reindeer *Rangifer tarandus constantini* Flerov, 1934 from the Late Pleistocene of Cosouti (Moldova).

toothed and small-sized reindeer similar to *R. tarandus constantini* are yielded by the Late Paleolithic sites of Kostenki, European Russia (20-30 kya), Cosouti, Moldova (11 – 20.4 kya), Rascov-8, Moldova (18 – 21 kya), and l'Aven des Planes, South France (final stage of Würm) (Croitor 2010). Apparently, the enlisted European Paleolithic sites indicate the chronology of the dispersal of *R. tarandus constantini* westward during the Last Glacial phase.

R. tarandus constantini represents an extreme adaptation of reindeer to grazing in the open dry periglacial environment. Possibly, the food habits of this subspecies were similar to those of the fossil reindeer from Alaska that displayed a heavy occlusal tooth wear for young and adult animals that reflects a very abrasive diet (Rivals & Solounias 2007). Unlike modern reindeer, the volume of nasal cavity of *R. tarandus constantini* is rather small indicating that the Paleolithic reindeer did not evolve yet adaptations to cold air breathing (Flerov 1952). The function of increased nasal cavity is air warming and moistening before its entrance to the trachea and lungs. Nasal cavity is correlated with muzzle breadth and the maximal volume of nasal cavity is recorded in modern arctic reindeer (Flerov 1952; Sokolov 1995).

Despite of several taxa created for fossil reindeer, some of Late Pleistocene reindeer forms remain unnamed. This is the case of the large reindeer from Duruitoarea Veche [layer II] and Brînzești-1 [III] (Moldova) is an archaic form of reindeer that arrived in Europe during the earlier expansion events of the species. It equals in size the modern forest North American subspecies *R. tarandus caribou* and *R. tarandus terranova* (Croitor 2010). The fossil reindeer in question is characterized by rather long metapodials with narrow epiphyses, indicating an adaptation to the wooded landscape. Cheek teeth are larger than in modern *R. tarandus tarandus*, but smaller than in *R. tarandus constantini*. Nonetheless, it is difficult to give an exact systematic and paleoecological interpretation for reindeer remains from Paleolithic sites, since the osteological material in most cases is very fragmented and could be biased by the selective hunting of Paleolithic man. The male remains attain 50% of the sample number in Duruitoarea Veche [II] and 41% in Brînzești-1 [III], therefore the presence of males in the samples is much higher than in a natural reindeer population and may indicate a hunting selection of the Paleolithic man in the favor of large individuals (Croitor 2010).

The origin of reindeer was associated with North American continent or Beringia (Flerov 1952; Geist 1988), however, this hypothesis was not confirmed by the paleontological record (Bondarev et al. 2017). The recent discovery of a frontoparietal skull fragment of *Rangifer sp.* from the Early Pleistocene of Isakovka-4 (Omsk, Russia) dated back to 2.1-1.8 Ma allows to regard Northern Eurasia as a possible center of reindeer origin (Bondarev et al. 2017). The specimen from Isakovka-4 is characterized by the typical for reindeer frontoparietal suture and the short and broad braincase, while the pedicles, unlike modern reindeer, are inclined backward and set parallel to each other, demonstrating the primitive for cervids morphological condition. The associated fauna and flora indicate rather warm climate conditions (Bondarev et al. 2017). The finding

from Isakovka-4 is exceptional and may suggest that that reindeer belongs to the old capreoline radiation in Northern Eurasia or just had a dispersal event into Eurasia during Early Pleistocene.

Anyway, all known Middle and Late Pleistocene reindeer of Eurasia share with the advanced American barren-ground caribou a peculiar specialized antler shape with the short distance between the first and second tines (Fig. 11) that permitted Geist (1998) to assume that all reindeer from the Middle and Late Pleistocene of Old World stem from this advanced North American form. According to Geist (1998), the first immigration event of reindeer in Eurasia occurred during the Riss Glaciation. Geist (1998) regards the barren-ground caribou as a forerunner for all modern Eurasian subspecies of reindeer. The genetic gap between the tundra subspecies *R. tarandus tarandus* and the forest subspecies *R. tarandus fennicus* is not as large as the North American forest caribou and barren ground caribou. According to the mitochondrial DNA analysis, the modern Eurasian tundra and forest subspecies have the diphyletic origin from a smaller refugium in western Eurasia situated in close connection to the extensive ice sheet that covered Fennoscandia, and a larger refugium of Beringia (Røed 2005). The paleontological seems to be in accordance with genetic data: apparently, the origin of the fossil reindeer with relatively small teeth known as "*R. tarandus guettardi*" took place in the smaller Western refugium, while the origin of *R. tarandus constantini* is related to the Beringian refugium. During the last glacial maximum, *R. tarandus constantini* dispersed westward and mixed with local European reindeer forms.

Rankama & Ukkonen (2001) suggest that Western Europe is the area of origin of modern tundra reindeer. Possibly, the reindeer from Villestofte is such a transitional form between large-toothed Upper Pleistocene reindeer and modern *R. tarandus tarandus*. Specific adaptations of *R. tarandus fennicus* to forest habitats were evolved quite recently after forest extension in the postglacial time and have a secondary character (Geist 1998; Røed 2005). According to Rankama & Ukkonen (2001), the origin of forest reindeer could be related to the forested refugium in the East from Fennoscandia. This hypothesis finds its support in Alekseeva (1990), who mentioned a finding of fossil reindeer skull from Tatarstan (Russia) similar to modern *R. tarandus fennicus*.

SUBFAMILY CERVINAE GOLDFUSS, 1820

Genus *Euprox* Stehlin, 1928*EUPROX PIDOPLITSCHKOI* (KOROTKEVICH, 1964)**Synonymy:**

1964 *Eostyloceros pidoplitschkoi* sp. nov.: Korotkevich, p. 807, fig. 1.

1965 *Muntiacus pliocaenicus* sp. nov.: Korotkevich, p. 107, fig. 2.

1968 *Muntiacus polonicus* sp. nov.: Czyżewska, 1968, p. 582, Pl. VIII, figs. 3-4.

Korotkevich (1964b) described a small two-pointed antler attached to a short pedicle from the Pliocene of Trifești (wrongly spelled by Korotkevich as Trifonești), Southern Moldova, as a new muntiacine deer *Eostyloceros pidoplitschkoi*. According to Korotkevich (1964), the simple antler bauplan combined with the short pedicle approach this cervid form to the genus *Eostyloceros* Zdansky, 1925 from the Late Tertiary of China. Later, Korotkevich (1970) ascribed to this species a series of similar antlers from the Early Pliocene of Kuchurgan, Ukraine (Fig. 12). From the same Kuchurgan deposits, Korotkevich (1965a) described another muntjac-like deer *Muntiacus pliocaenicus* based on few poorly preserved antlers with frontal bones characterized by the somewhat longer pedicles and, according to the interpretation of Korotkevich, the frontal bony ridges as in modern muntjacs. Korotkevich (1965a, 1970) regarded the so-called “frontal bony ridges” in *Muntiacus pliocaenicus* as an essential diagnostic character that approach the

cervid remains in question to modern *Muntiacus*. Croitor (2014) tentatively included *E. pidoplitschkoi* and *M. pliocaenicus* in the genus *Euprox*, since the morphology of their antlers show a strong resemblance with Miocene *Euprox furcatus*. Actually, the rather weak roll-shaped structures on the lateral side of the frontal bones between pedicles and orbits are common for cervids and do not correspond to the sharp bony ridges characteristic for the modern representatives of the genus *Muntiacus*, which range from pedicles to nasal bones and represent a specific adaptation for eye protection during the intraspecific male combats (Croitor 2014). The figure 13 shows the material described by Korotkevich (1964b, 1965a, 1970) as *Eostyloceros pidoplitschkoi* and *Muntiacus pliocaenicus* from Kuchurgan represents a rather compact cluster, while the type specimen from Trifești has a detached position due to its robust pedicle. Possibly,

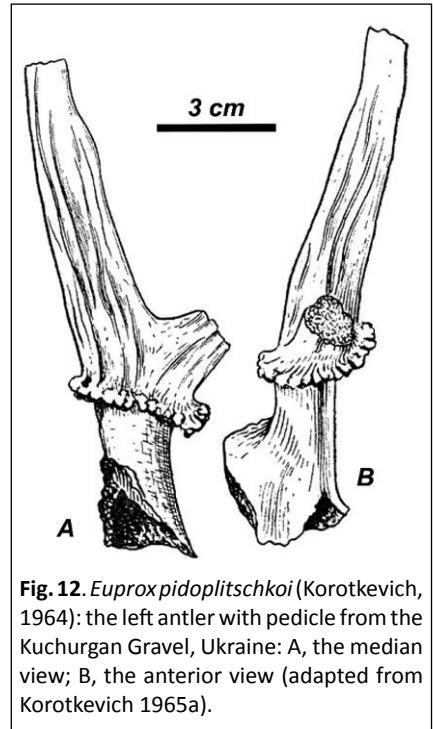


Fig. 12. *Euprox pidoplitschkoi* (Korotkevich, 1964): the left antler with pedicle from the Kuchurgan Gravel, Ukraine: A, the median view; B, the anterior view (adapted from Korotkevich 1965a).

the specimen from Trifești belongs to an old individual, or represents a more evolved form, taking in consideration the some-what younger geological age of the Carbolian sands (Pevzner et al. 1996; Vangengeim & al. 1998, 2005). The most important is that the specimens described by Korotkevich (1970) as *Eostyloceros pidoplitschkoi* and *Muntiacus pliocaenicus* represent a homogenous sample. The material of muntjac-like deer from Kuchurgan is very poor and incomplete, however, one can notice that *Eostyloceros pidoplitschkoi* and *Muntiacus pliocaenicus* are distinguished only by a small difference in their pedicle length and most probably represent the different ontogenetic stages of the same cervid form (Croitor 2014). Therefore, these species names are considered here as synonyms.

Czyżewska (1968) established another species *Muntiacus polonicus* based on a juvenile mandible from the Early Pliocene of Węże-1. Both names *M. pliocaenicus* and *M. polonicus* were maintained, since the direct comparison of those species based on different skeletal parts was not possible (Croitor & Stefaniak 2009). Since *Muntiacus polonicus* comes from the roughly coeval Early Pliocene fauna of Węże-1, this species name is also included here in the synonymy of *Euprox pidoplitschkoi* (Korotkevich, 1964). The difference in pedicle length between *Euprox pidoplitschkoi* and *Euprox furcatus* is equivalent to the difference between *Muntiacus muntjac* and *Muntiacus reevesi* (Fig. 13).

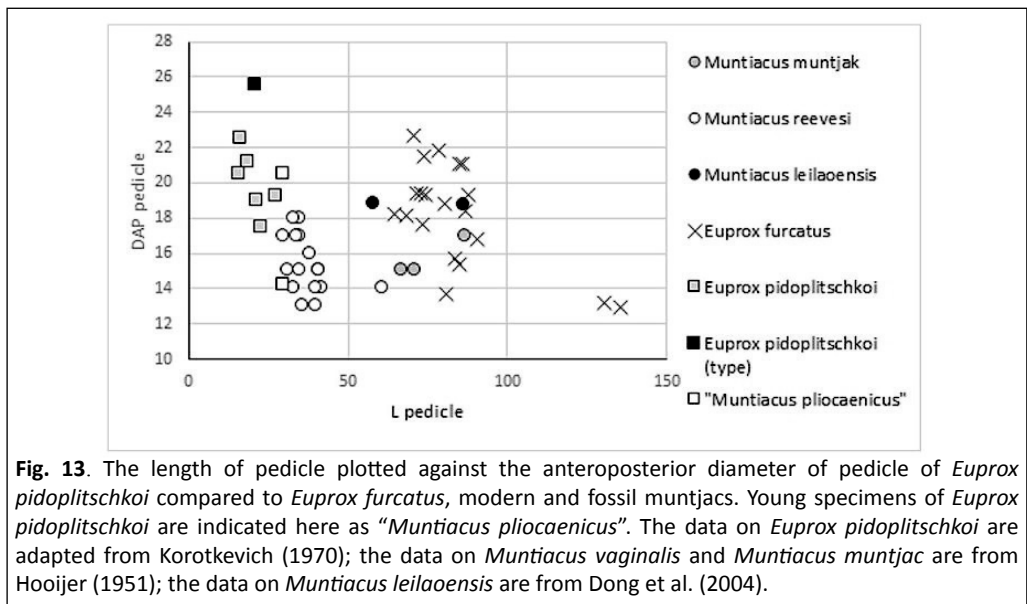


Fig. 13. The length of pedicle plotted against the anteroposterior diameter of pedicle of *Euprox pidoplitschkoi* compared to *Euprox furcatus*, modern and fossil muntjacs. Young specimens of *Euprox pidoplitschkoi* are indicated here as "*Muntiacus pliocaenicus*". The data on *Euprox pidoplitschkoi* are adapted from Korotkevich (1970); the data on *Muntiacus vaginalis* and *Muntiacus muntjac* are from Hooijer (1951); the data on *Muntiacus leilaensis* are from Dong et al. (2004).

Euprox pidoplitschkoi is a very small deer (18 kg) as modern *Muntiacus reevesi*. The antlers are two-pointed with a low position of bifurcation. The posterior tine is stronger and longer than the anterior one, and is oriented along the axis of pedicle (Fig. 12). The antler surface is sculptured with sharp and deep ridges and furrows. A specific rugosity is often seen on the medial surface of antler base. The cross-section of antler tines is often sub-triangular (Fig. 14) as in modern *Muntiacus muntjac*. Nonetheless, antlers and pedicles are significantly more robust than in *Muntiacus* (Croitor & Stefaniak 2009).

The size and shape of the mandible from Weze (Nr. 99-Węże-1, IZW) are almost identical to those of modern *Muntiacus*. The DP₃ is characterized by the anteroposteriorly elongated metaconid that distinguishes this specimen from modern *Muntiacus* characterized by a small simple metaconid. DP₄ is supplemented with two ectostylids. The mandible from Weze is also distinguished from the Middle and Late Miocene *Euprox* by the absence of *Palaeomeryx* fold and smaller size. The ectostylids of lower molars are well-developed. The length of lower tooth row (deciduous teeth and molars) is about 62.3

mm. The occlusal length of molar series amounts to 35.9 mm. The upper molar (M³) Nr. 254 from Węże-1 is partially destroyed. The entostyle is not developed; the additional enamel fold of hypocone is well-developed. The metaconid has a particularly well expressed metastyle (the posterior labial rib) and the middle labial rib. This character approaches the specimen under study to modern muntjacs, which show the similar morphology. The length of the molar crown is 9.8 mm (measured at the tooth base), the basal labiolingual breadth of the tooth amounts to 11.5 mm.

The close phylogenetic relationship of *Euprox pidoplitschkoi* with Asian *Muntiacus* is improbable. The earliest known muntjac *Muntiacus leilaoensis* from the Late Miocene of southwestern China is already specialized and shows all diagnostically important characters of modern *Muntiacus*: the pedicles are very long, the frontal bones are bordered with sharp frontal bony ridges, the main antler beam is long, while the anterior tine is very small (Dong et al. 2004). The triangular cross-section of antler branches in *Euprox pidoplitschkoi* approach this cervid to *Euprox furcatus* (the estimated body mass is 33-38 kg). According to Mennecart et al. (2017), the bony labyrinth morphology of both *Euprox furcatus* and "*Cervus*" *ruscinensis* Deperet, 1890 define them as early offshoots of the subfamily Cervinae. *Euprox pidoplitschkoi* is distinguished from "*Cervus*" *ruscinensis* (possibly, is a junior synonym of "*Cervus*" *australis* De Serres, 1832) from the Pliocene of Roussillion, France, by the smaller body size, the longer pedicles, the triangular cross-section of antler branches, and the lower position of ramification; in "*Cervus*" *ruscinensis*, the ramification is presented by a primordial knob at 7 cm from the burr (Deperet 1890). One can assume that *Euprox pidoplitschkoi* is an archaic Pliocene descent of the somewhat larger representative of the subfamily Cervinae *Euprox furcatus* that dispersed into western Eurasia during Middle Miocene.

Euprox pidoplitschkoi is known from the Ruscinian fauna of Poland, Ukraine and Moldova (MN 14 and MN 15) (Croitor & Stefaniak 2009). Some scant remains of "*Muntiacus*" are reported from MN 15 of Romania (Radulesco et al. 2003) and MN 16a of Slovakia (Fejfar et al. 1990). The earliest remains of *E. pidoplitschkoi* are known

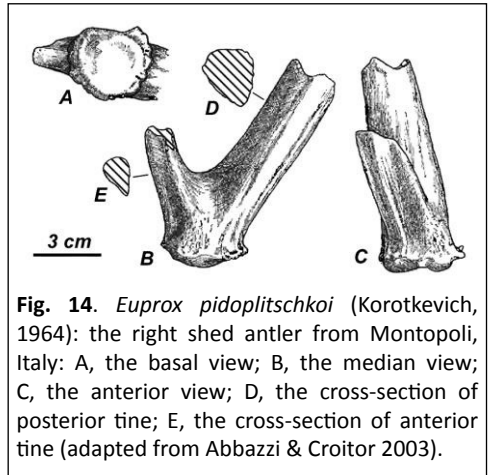


Fig. 14. *Euprox pidoplitschkoi* (Korotkevich, 1964): the right shed antler from Montopoli, Italy: A, the basal view; B, the median view; C, the anterior view; D, the cross-section of posterior tine; E, the cross-section of anterior tine (adapted from Abbazzi & Croitor 2003).

from very beginning of Ruscinian or even end of MN13 of Ukraine, Moldova, and Bulgaria (Korotkevich 1988; Spassov 2005). The exact age of the shed antler of *Euprox pidoplitschkoi* from Montopoli, Italy, remains unclear (Abbazzi & Croitor 2003). The known area of distribution ranges from Central Italy to North Black Sea Area, including Balkans.

Genus *Metacervocerus* Dietrich 1938

Dietrich (1938) proposed the subgenus *Cervus* (*Metacervocerus*) Dietrich 1938 with the type species *Cervus pardinensis* Croizet & Jobert, 1828 for Late Pliocene primitive small-sized *Axis*-like cervines of Europe with simple three-pointed antlers. Samson et al. (1970) elevated *Metacervocerus* to the generic level. The type species of *Metacervocerus* is still imperfectly known: only antlers and tentatively associated mandibles and upper molars with lingual cingulum are known (Heintz 1970). There are several conflicting opinions about the systematic position of the primitive small-sized cervines with long pedicles and three-pointed antlers. According to De Vos et al. (1995), *Metacervocerus pardinensis* and *Metacervocerus rhenanus* belong to the genus *Cervus*, while Pfeiffer (1999) included them in the genus *Dama*. However, the skull shape of *M. rhenanus* is too primitive to be included in *Dama* or *Cervus*. Unlike *D. dama*, the pedicles of *Metacervocerus* are longer and sloped backward, the braincase is relatively long and little flexed, the bullae tympani are relatively smaller (Croitor 2006a). Unlike *Cervus elaphus*, *M. rhenanus* is characterized by the relatively longer braincase and the shorter orbitofrontal portion, the relatively longer nasal bones, which are extended behind the line connecting anterior edges of orbits, the broad bell-shaped basioccipitale, the larger bullae tympani and the missing upper canines. Di Stefano & Pentronio (2002) included *M. rhenanus* and *M. pardinensis* in the modern genus *Rusa*; however, this viewpoint is not supported by the cranial morphology. Unlike *Metacervocerus*, *Rusa* is characterized by the short nasal bones, which do not reach the level of anterior margins of orbits, the small bullae tympani, the narrow basioccipitale (as *Cervus*), and possess the upper small canines (as *Cervus*) that should be regarded as a primitive character (Flerov 1952). Therefore, *Metacervocerus* and *Rusa-Cervus* represent two different evolutionary lineages of Cervinae distinguished by an incompatible mosaic combination of the primitive and advanced characters. The analysis of bony labyrinth morphology carried out by Mennecart et al. (2017) confirmed the hypothesized by Croitor (2014) sister phylogenetic relationship of *M. rhenanus* (= *M. philisi*) with modern *Axis axis*.

METACERVOCERUS PARDINENSIS (CROIZET & JOBERT, 1828)

This is a small cervid (the estimated body mass is about 60 kg) with simple three-pointed antlers described first from the Pliocene of Perrier-Etouaires, France (Pomel 1853). The neotype designated by Heintz (1970) is a left shed antler (Fig. 15). The antler base is circular; the diameter of burr is 49.0 mm. The beam above the burr is slightly compressed from the sides (DAP×LDM = 38.6×35.1 mm). The antler beam slightly deviates from the burr backward and sideward and is gently curved. The first tine is situated at 70.0 mm (median measurement) or 65.8 mm (lateral measurement)

from the burr. The antler beam is cylindrical (DAP×LDM above the first ramification = 29.1×27.7 mm). The distal bifurcation is set in the parasagittal plane; the posterior tine of distal bifurcation is stronger and longer than the anterior one. The total length of the antler exceeds 56 cm. The additional material provides the following characteristics: the pedicels are long (L>D) and sloped backward from the face as in modern *Hyelaphus* or *Rusa*. The dentition is rather primitive: the upper molars are supplemented with a strong cingulum and have very oblique lingual wall. The angle between the lingual and labial walls in M² is wider than 40°. The morphology of P₄ is primitive.

The oldest remains come from the Late Ruscian (MN15) faunas of Moldova (Croitor & Stefaniak 2009) and Bulgaria (Spasov 2005). Some poor remains attributable to *M. pardinensis* are reported from MN15b of Braşov Depression, Romania (Radulesco et al. 2003) and Poland (Stefaniak 1995, 2015). The younger remains are also reported from Romania (Radulesco et al. 2003; Radulesco 2005) and Slovakia (Sabol 2003) dated by MN16a. The youngest remains of this species are reported from the type locality of Les Etouaires (France) and the Red Crag Nodule Bed (England), MN16b (Lister 1999). A similar to *M. pardinensis* shed antler (DAP×DLM above the burr is 40.3×38.5 mm, the height of first ramification is 79.2 mm) was reported by Alekperova (1964) from the Upper Pliocene of Azerbaijan as *Cervus (Rusa) sp.*

METACERVOCERUS RHENANUS (DUBOIS, 1904)

Dubois (1904) introduced the species name *Cervus (Axis) rhenanus* for a small-sized deer from Tegelen. The original publication of the species name is accompanied by a figure of the type specimen but not by any description. According to Spaan (1992), *Cervus philisi* Schaub, 1941 is a junior synonym of *Cervus rhenanus* Dubois, 1904. Croitor & Bonifay (2001) included the species under study in the genus *Metacervocerus* Dietrich, 1938.

The antlers are three-pointed, long, and thin. The total antler length in the skull CEY-2-2318 from Ceysaguet (France) amounts to 760 mm (*dext*) and to 767 mm (*sin*). The distance between the antler base and the top in the same specimen amounts to 710 mm (*dext*) and to 732 mm (*sin*). The distance between tops of the antler amounts to

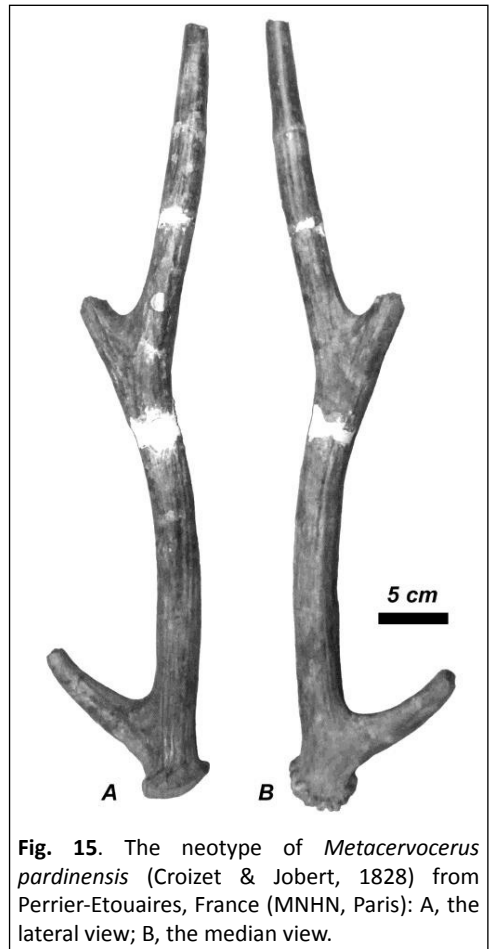


Fig. 15. The neotype of *Metacervocerus pardinensis* (Croizet & Jobert, 1828) from Perrier-Etouaires, France (MNHN, Paris): A, the lateral view; B, the median view.

565 mm. The proximal parts of antler beams form an angle of 70° . The second third of antlers is bow-shaped and more divergent. The distal portions of antlers are more or less parallel each to another. The angle of first ramification amounts to 60° . The basal tine is situated at a certain distance from the burr. The distal bifurcation is oriented in the parasagittal plane and formed by the second tine inserted on the anterior side of the beam. The antler beam becomes compressed laterally in the area of the distal bifurcation. The antler surface may be depressed from the sides in the area of the bifurcation. The angle of distal bifurcation amounts approximately to $40\text{--}45^\circ$. The transversal section of antler tines is circular. The antler surface is pearled and sculptured with longitudinal ribs and furrows. The angle of the first ramification of antler is one of the variable character and varies from 60° to 100° (Croitor 2006a). The height of first ramification varies in the sample from Ceysaguet from 41.6 mm to 83.5 mm.

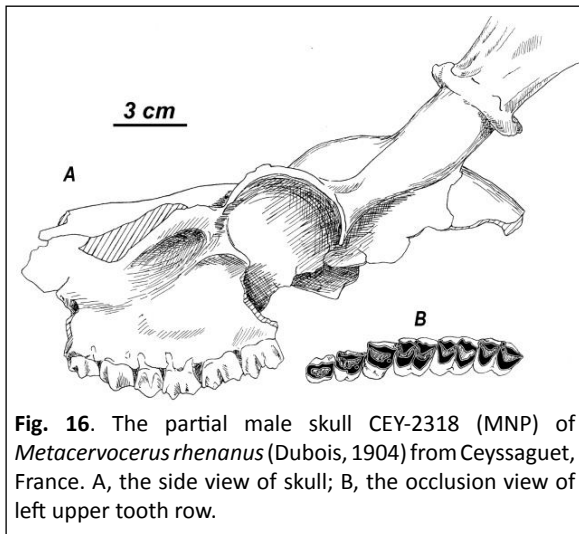


Fig. 16. The partial male skull CEY-2318 (MNP) of *Metacervocerus rhenanus* (Dubois, 1904) from Ceysaguet, France. A, the side view of skull; B, the occlusion view of left upper tooth row.

The profile of frontal bones is concave at the level of the anterior half of orbits. The anterior part of each frontal bone is slightly swollen. The long pedicles are slightly dorso-ventrally compressed and sloped backward from the face (Fig. 16). The anterior edge of orbits projects down to M^2 (Figs. 16, 17). Nasal bones are comparatively long and extend behind the line connecting the anterior edges of orbits. The preorbital fossae are large and deep. The ethmoidal openings are large. The ethmoidal openings are very large and their border with the nasal bones may be long (as

in the female skull from Sénèze Nr. 210638, PMUL) or very short (the sample from Ceysaguet). The articulation between nasal and premaxillary bones is long (23 mm in the skull Nr. 210638, PMUL) as in *Cervus*, and much longer than in modern *Dama dama*. The braincase is elongated, unflexed and not rounded as in *Dama* (Fig. 17). The braincase is long as in *Axis*, and much longer if compared to *Cervus* and *Dama*. Bullae tympani are rounded, smooth, but not as large as in *Dama*. The face length measured from the anterior edge of orbits to prosthion amounts to 56.9% of the condylobasal length in the female skull Nr. 210638 and is relatively longer than in *Hyelaphus porcinus* (51.3 – 54.7%, n=5) and *Cervus nippon* (52.8 – 55.1%, n=3), and falls within the variation range of *Axis axis* (50.4 – 57.8%, n=4). The cranial proportions of *Metacervocerus rhenanus* and such morphological peculiarities as the long pedicles and rather large and rounded bullae tympani approach the deer under consideration to modern *Axis*. However unlike *Axis*, *Metacervocerus rhenanus* shows such a derived character as the long caudally extended nasal bones.

The mandible Nr. 209564 (PMUL) from S n ze is characterized by a rather long diastema, which is slightly longer than the series of lower molars. It is comparatively longer than in *Cervus nestii*, *Cervus nippon* and *Dama dama*, however, is shorter if compared to *Hyelaphus porcinus* and *Cervus elaphus*. The ratio between premolars and molars vary from 61.4 to 65.8% (n=7; M = 63.5%). The processus angularis is strong.

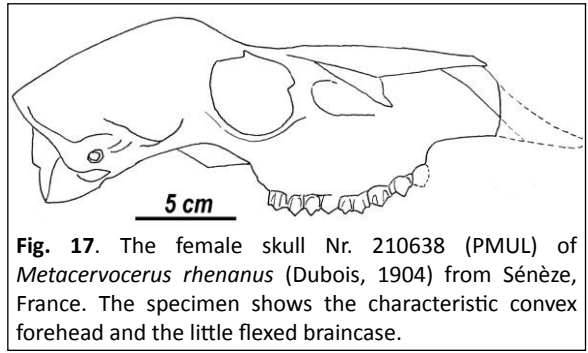


Fig. 17. The female skull Nr. 210638 (PMUL) of *Metacervocerus rhenanus* (Dubois, 1904) from S n ze, France. The specimen shows the characteristic convex forehead and the little flexed braincase.

The hypocone and protocone of P^2 are separated. The hypocone of P^2 has an internal enamel fold. The lingual wall of P^3 has a vertical groove separating the merged hypocone and protocone. The hypocone of P^3 has an internal enamel fold as well. There is no separation of hypocone and protocone in P^4 .

Upper molars may show a weak trace of cingulum and are supplemented with the protoconal enamel fold and the eperon. A weak continuous cingulum is recorded only in three specimens (all M^3) of the sample from S n ze. In the majority of remains (22 specimens) the cingulum is interrupted or completely reduced. The cingulum seems to be more frequent in the sample from Vallonnet (RMPM). The individual variation of P_4 is studied in the sample from Ceysaguet. The extended caudally metaconid of P_4 is merged in some cases with entoconid. The contact between metaconid and paraconid was never observed. The crown of I_1 is very wide, triangle shaped, asymmetric with extended and acute lateral angle. I_2 , I_3 and C are smaller and very narrow (Croitor 2006a).

The upper isolated molar M^3 R12079 from Vallonnet (RMPM) is characterised by a very oblique lingual side that forms with the labial surface of tooth an angle of 45° and a clear cingulum that borders the basal part of protocone. The posterior wing of protocone has an additional enamel fold. This combination of characters is found in several isolated teeth. The left hemimandible Nr. 416 (RMPM) is characterised by primitive P_4 .

Metacervocerus rhenanus is a long-lasting Early Pleistocene species that changed very little from its first occurrence 2.5 Ma in Saint-Vallier (France) to its last record 0.9 Ma in Vallonnet. The area of distribution includes Spain, France, the Netherlands, Romania, Greece (Croitor & Bonifay 2001). The absence of this species on the Italian Peninsula is remarkable.

Genus *Praeelaphus* Portis 1920

Portis (1920: 133) proposed the subgenus *Cervus* (*Praeelaphus*) for epy Early Villafranchian species *Cervus arvernensis* Croizet & Jobert, 1828, *Cervus perrieri* Croizet & Jobert 1828, and *Cervus etueriarum* Croizet & Jobert, 1828 from Perrier (France). Grubb (2000) supposed that *Praeelaphus* Portis may be synonymous with *Metacervocerus* Dietrich, however, this is not the case: *Praeelaphus* and *Metacervocerus* are based on

two different valid species: *Cervus perrieri* and *Cervus pardinensis* respectively. Heintz (1970) placed *Cervus perrieri* in the arbitrary group *Cervus sensu lato*, therefore its systematical position remained uncertain. The taxonomical solution was proposed much later (Croitor 2012): the genus *Praelaphus* Portis, 1920 with type species *Cervus perrieri* is proposed for small to medium-sized Pliocene – Early Pleistocene cervines with primitive dental morphology and advanced shape of four-pointed antler with frontally oriented flattening of distal portions of antler beams.

The genus includes several deer species from Pliocene and Early Pleistocene of Europe close in size to modern red deer and fallow deer. Pedicles are of moderate length (the posteromedian length of pedicle in adult males does not normally exceed its diameter) and slightly compressed anteroposteriorly. Fully grown antlers are large with respect to the animal size, four-pointed. The first tine is situated above the burr at a distance larger than the diameter of the antler base. The antler beam often forms well-expressed flattened extensions in the areas of ramification. The transversal section of the beam below the second tine is not regular, often pyriform or ovoid. The beam above the second tine is significantly compressed and forms an extended flattening with the frontal or oblique orientation. Correspondingly, the distal bifurcation may be oriented in the frontal or oblique plane. The dentition is primitive: P_4 is generally simple, with a low degree of molarization, the lower premolar series is relatively long compared to molars and normally is longer than in *Cervus* and *Dama* (Croitor 2012).

PRAELAPHUS PERRIERI CROIZET ET JOBERT,
1828

This is a medium-sized deer (ca. 180 kg) with large four-pointed antlers and primitive dental morphology reported from Late Pliocene of France and England (MN16b). The well-preserved cranial material of this species is unknown. Pomel (1853) published the first brief description of deer species (*Cervus perrieri* Croizet & Jobert, 1828, *Cervus etueriarum* Croizet & Jobert, 1828, and *Cervus issiodorensis* Croizet & Jobert, 1828) based on fossil remains from Perrier figured by Croizet & Jobert (1828). According to Heintz (1970), *C. etueriarum* is based on juvenile antlers of *C. perrieri*. *Cervus arvernensis* was based on a poor fragment of antler with low insertion of the basal tine and most probably it also falls

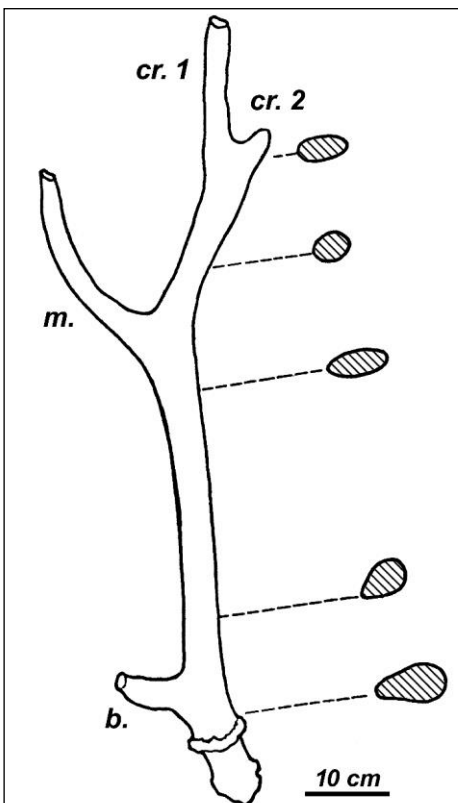


Fig. 18. Right antler (neotype) of *Praelaphus perrieri* (Croizet & Jobert, 1828) from the Late Pliocene of Les Etouaires, France (adapted from Heintz 1970).

within the individual variation of *Cervus perrieri* (Cotoior 2017). *Cervus issiodorensis* Croizet & Jobert, 1828 is another poorly known species that falls in the synonymy of *C. perrieri*: it is represented by the shed antler Nr. 211214 (PMUL) with a rather low insertion of the short and compressed from sides basal tine and the pyriform shape of the beam cross-section. Heintz (1970), who published the first revision of *Cervus perrieri*, could not find any specimen in the collection of MNHN that corresponds rigorously to the specimen figured by Croizet & Jobert (1828: pl. IV, fig. 1) and chooses a neotype that better corresponds to the original figure and possibly represents the same specimen (Fig. 18). The pedicle of this specimen is relatively long ($L > D$); the burr is well-developed. The cross-section of both pedicle and burr are circular. The antler beam becomes compressed from the sides above the burr; the first tine is situated rather high above the burr. The antler beam bears a well-expressed longitudinal groove from the lateral side between the first and second ramifications. The anteromedial side of the beam also bears a longitudinal groove-like depression, so the cross-section of the beam in this part of the antler is pyriform. The distance between the second and third ramifications is significantly longer than the distance between the first and second ramifications. The antler beam becomes compressed above the second ramification. This flattened part of beam is terminated by the distal fork. The plane of the flattened portion of the beam is often perpendicular with the plane of the second ramification but this character may be variable. Heintz (1970) ascribed upper molars devoid of the lingual cingulum to the species in question. Lower mandibles and postcranial bones of *Praeelaphus perrieri* are practically undistinguishable from the remains of *Arvernoceros ardei* from the same locality. Both species are distinguished only by antler morphology and are characterized by the similar body size. It is worth mentioning, that all lower mandibles from Perrier are characterized by a relatively long premolar series: the premolar/molar ratio of the mixed sample varies between 64.3% and 70.8%.

PRAEELAPHUS LYRA (AZZAROLI, 1992)

Azzaroli (1992) described a fine pair of antlers from Ponte a Elsa (Central Italy) as a new species *Pseudodama lyra* in the composition of the Triversa faunal unit (Pliocene, MN16, ca. 3.2 Ma: Gliozzi et al. 1997). According to Azzaroli (1992), the deer from Ponte a Elsa is a transitional evolutionary stage between Villafranchian deer of the *pardinensis-rhenanus* type with three-tined antlers and *Pseudodama nestii* with four-tined antlers. Later, de Vos et al. (1995) regarded "*Pseudodama*" *lyra* as a junior synonym of *Metacervoceros rhenanus* (= *Cervus rhenanus*: de Vos et al., 1995). However, the specimen from Ponte a Elsa shows a set of morphological differences from antlers of *M. rhenanus*. Unlike "*Pseudodama*" *lyra*, the antlers of *M. rhenanus* are sculptured with a pearling and longitudinal ribs and furrows, the apical tine is always cylindrical and its dorso-ventral compression has never been observed, the antler beams are less diverged and not bent inward. The asymmetry of the distal portions of the antlers from Ponte a Elsa suggest the instability of this character. Croitor (2006a) supposed that "*Pseudodama*" *lyra* is a junior synonym of *Cervus nestii* (Azzaroli), however, the new data indicate that the resemblance between those two Italian deer is superficial (Croitor 2014).

The holotype IGF1934v (MGUF) from Ponte a Elsa (Azzaroli 1992: pl. 1, fig. 1) represents a complete pair of antlers with pedicels and frontal bones. The first tine springs off rather high above the burr and forms with the beam an angle of 60°. The first tine is thin, cone-shaped, curved, and slightly deviates sideward. The angle of divergence between first segments of the antler beams is of 100°. The first segment portion of antler is rather long and cylinder-shaped. The cross-section of antler beam segment between the first and the second tines is irregular as in *Praeelaphus perrieri*; the antler surface is rather smooth. The distal portion of beam above the second tine is short, curved inward and compressed anteroposteriorly. The tip of the right antler is sharp, while the top of the left antler is ended by two small prongs oriented in a frontal plane. The length of right and left antlers amounts to 73 cm and 78 cm respectively. The antler surface is rather smooth. The pedicles are moderately long and compressed anteroposteriorly. The breadth of skull behind pedicels amounts to 108.0 mm.

The antlers of *Praeelaphus lyra* (Azzaroli, 1992) remind those of *Praeelaphus perrieri*, but are more slender. The holotype of *Praeelaphus lyra*, apparently, belongs to a young individual and did not achieve the full degree of development: the antlers are characterized by specific for *P. perrieri* and *P. warthae* flattening of the distal beam segment, but the distal bifurcation is not developed yet.

Apparently, the earliest remains of this cervid come from Eastern Europe. Some poor antler remains from the Early Pliocene of Moldova (MN15) are ascribed to *Praeelaphus lyra* (Croitor & Stefaniak 2009).

PRAEELAPHUS WARTHAE (CZYŻEWSKA, 1968)

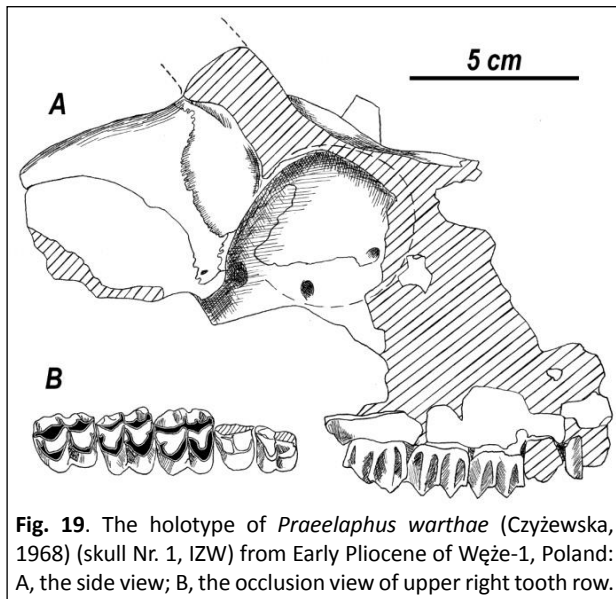


Fig. 19. The holotype of *Praeelaphus warthae* (Czyżewska, 1968) (skull Nr. 1, IZW) from Early Pliocene of Węże-1, Poland: A, the side view; B, the occlusion view of upper right tooth row.

Praeelaphus warthae is a rather medium-sized deer (the mean estimated body mass is 120 kg; the body mass of the largest individual is 145 kg) from the Late Ruscinian (MN15) of Poland based on a fragmented skull Nr. 1 (IZW, Fig. 19) of a young adult male with full permanent dentition that shows some wear. The skull fragment is represented by a part of the braincase, frontal bones with destroyed pedicels and right maxilla with P³-M³. The parietal bones are slightly convex; the orbito-frontal part of the skull is short; the anterior edge of the orbit is situated above M²/M³.

The pedicles are sloped backward. The frontal profile is convex in the area between the pedicle bases and then it is depressed between the

orbits. The frontal bones, in their turn, are somewhat depressed in the area between the frontal suture, the pedicle base and the orbit, and slightly swollen in their anterior part that joints the nasal bones. The breadth of the frontal bone measured from the frontal contraction in front of the pedicles to the frontal suture amounts to 53 mm. The elongated supraorbital channel is situated about 25 mm medially to the frontal edge in the area of contraction, and 26 mm from the frontal suture. The associated cranial material from Węże-1 (IZW) provides the following cranial characteristics: the frontal bones are characterized by their swollen anterior part, the short orbito-frontal portion is short, the preorbital fossae are rather large and deep, the basioccipitale is broad and bell-shaped, the *bullae tympani* are round, smooth, and devoid of a bony thorn characteristic of *Cervus elaphus* (Croitor & Stefaniak 2009). Some additional measurements are provided by the skull fragment Nr. 362 (Czyżewska 1959: pl. III, fig. 1): the diameter of *bulla tympani* amounts to 15.5 mm; the breadth at pharyngeal tuberosities is 29.0 mm; the breadth of occiput is 89.0 mm; the height of occiput is 68.5 mm.

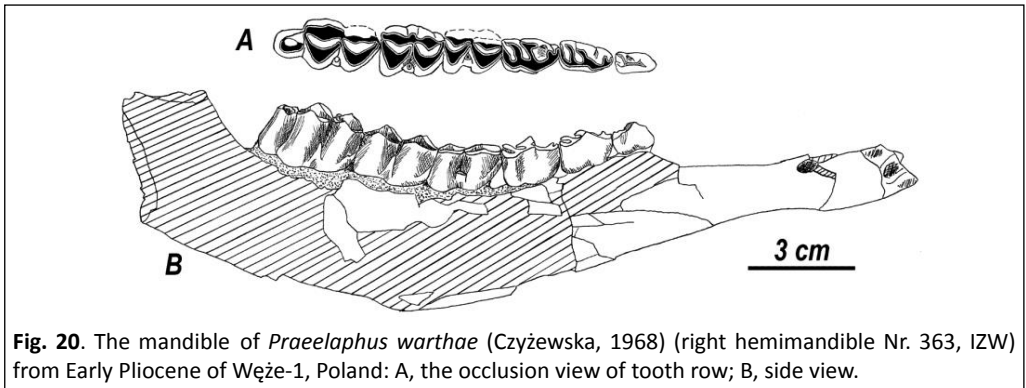


Fig. 20. The mandible of *Praeelaphus warthae* (Czyżewska, 1968) (right hemimandible Nr. 363, IZW) from Early Pliocene of Węże-1, Poland: A, the occlusion view of tooth row; B, side view.

Upper molars of the skull Nr. 1 (IZW) are characterized by the presence of a small entostyle, a hypoconal spur, a small enamel fold on the posterior wing of the protocone and an additional small interior enamel fold on the anterior wing of the protocone (Fig. 19, B). The upper third premolar (P^3) shows a cleft lingual wall and hypocone and protocone separated from each other. The hypocone is supplemented with an internal enamel fold. The lingual wall of the upper fourth premolar (P^4) is not cleft; its hypocone is supplemented with an internal bifurcated enamel fold. The lower fourth premolar (P_4) is primitive, with separated parastylid and paraconid (Fig. 20). The metaconid is extended anteroposteriorly, but it does not connect with paraconid and entoconid. Lower molars bear ectostylids. The *Palaeomeryx* fold is never present.

The fully-grown antlers of *P. warthae*, apparently, had four tines. The antler beam segment between first and second tine is cylinder-shaped, with circular or ovoid cross-section. The antler segment above the second tine is flattened and oriented in the frontal plane. One can assume that this flattening is terminated by a distal fork. The relative size of the lower tooth series of *P. warthae* is somewhat smaller than the sample of *perrieri-ardei* from Perrier-Etouaires (Croitor & Stefaniak 2009). Possibly, the

mandibles from Perrier-Etouaires with relatively shorter premolars belong to *P. perrieri*, which is closely related to *P. warthae*, while the lower mandibles with relatively longer premolar series belong to *Arvernoceros ardei*. The lower premolar series of *P. warthae* is comparatively longer than in modern *Cervus elaphus* and *Eucladoceros ctenoides* from S n ze, this demonstrating a more primitive condition of this character. The antler morphology of *P. warthae* reminds that of *Praeclaphus perrieri*. The difference in body size is the only character that distinguishes those two species. I do not exclude the possibility of synonymy of species names *perrieri*, *warthae*, and *lyra*, which, in fact, represent quite similar cervid forms.

PRAEELAPPHUS AUSTRALORIENTALIS CROITOR, 2017

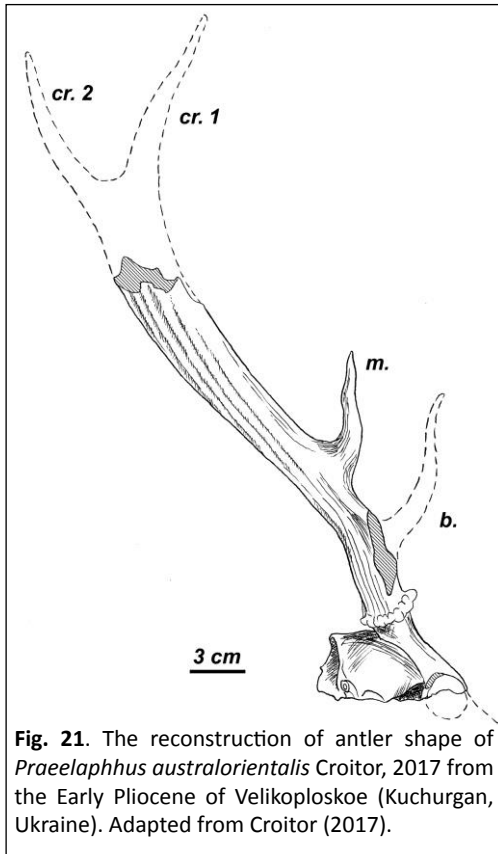


Fig. 21. The reconstruction of antler shape of *Praeclaphus australorientalis* Croitor, 2017 from the Early Pliocene of Velikoploskoe (Kuchurgan, Ukraine). Adapted from Croitor (2017).

This is a medium-sized deer (67 kg) from Early Pliocene (MN15) of Southeastern Europe (Ukraine, Romania). The species is characterized by the rather long braincase (the bregma – opisthocranium distance is longer than the braincase breadth behind pedicles in males), the comparatively narrow frontal bones in males (the braincase breadth measured behind pedicles attains ca. 80% of the frontal constriction before the pedicles; the same index in *P. warthae* is 73.7%), and the robust and moderately long pedicles (the length of the pedicle in mature males attains ca 2/3 of the pedicle lateromedial diameter). The position of pedicles shows a primitive condition: the pedicles are sloped backward and little divergent. The *bullae tympani* are quite small and characterized by an irregular shape (anteroposterior measurements: sin, 12.9 mm; dx, 13.2 mm), without any apical thorn or spike. The shape of the *bullae tympani* is quite similar to that of *Axis axis* described by Pocock (1943). The antlers are rather robust antlers with four tines

(Fig. 21). The shape of the cross-section of the antler base is circular and just slightly compressed in anteroposterior direction. Antler burrs are well developed and strong. The first and the second tines are inserted on the anterior side of the antler beam. The first tine is situated very high above the burr (the height of the first ramification exceeds more than two times the diameter of the basal part of antler beam). The antler segment between the first and the second tines is comparatively short (shorter than the height of the first ramification). The distance between the second and the distalmost

third ramification is three times longer than the distance between the first and the second ramifications. The basal segment of antler beam (below the first ramification) is regularly circular. The beam segment between the first and second ramifications has a longitudinal keel on the anterior side. The antler beam between the second and the third ramifications is significantly flattened, oriented in the parasagittal plane and terminated with a distal bifurcation. The anterior tine of the distal bifurcation is stronger and represents a continuation of the beam axis. *P. australorientalis* is the smallest species of the genus and seems to be morphologically most removed from the rest of *Praeelaphus* species: its first tine is inserted comparatively very high, much higher than in other forms of *Praeelaphus*, the beam segment between the first and the second tines is very short, while the flattened blade-like distal portion of beam is situated rather in parasagittal plane, not in frontal plane as in *Praeelaphus lyra*, *Praeelaphus warthae*, and *Praeelaphus perrieri*. However, the latter character may be variable in *Praeelaphus perrieri*.

PRAEELAPHUS SP. FROM OLIVOLA

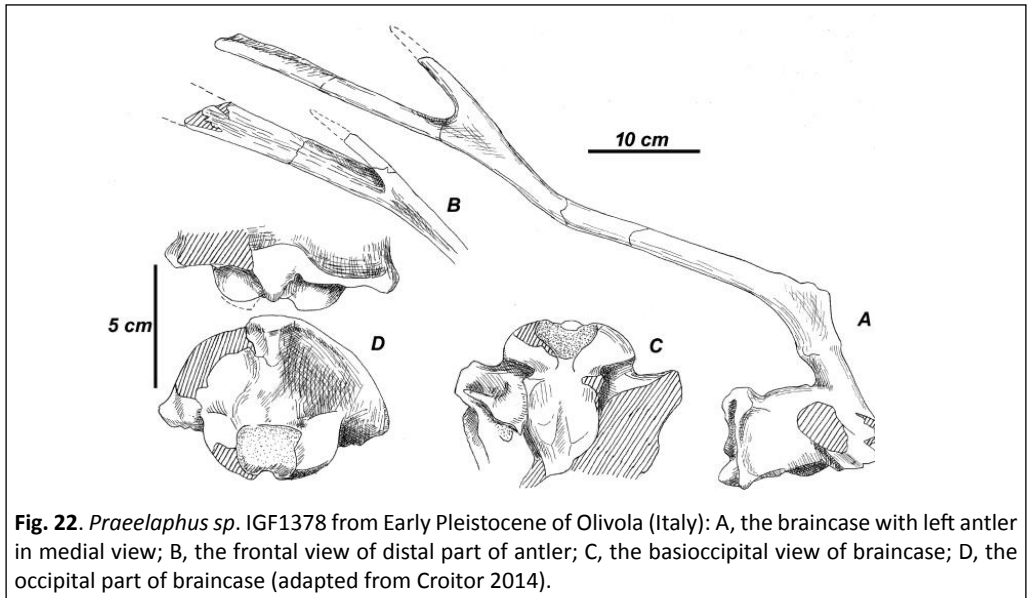


Fig. 22. *Praeelaphus* sp. IGF1378 from Early Pleistocene of Olivola (Italy): A, the braincase with left antler in medial view; B, the frontal view of distal part of antler; C, the basioccipital view of braincase; D, the occipital part of braincase (adapted from Croitor 2014).

One of the last representatives of the genus *Praeelaphus* comes from Olivola, a Late Villafranchian site (1.8 Ma) in Tuscany (Italy). The antlered braincase IGF1378 of *Praeelaphus* cf. *lyra* from Olivola was originally described by Azzaroli (1947: p. 52, fig. 1-7; p.55, fig. 4-1) as *Dama nestii nestii*. The braincase IGF1378 with left antler belongs to a mature male individual (sutures of braincase are obliterated) and shows the antler morphology characteristic for *Praeelaphus* (Fig. 22). Its braincase is slightly flexed and relatively short as in *Praeelaphus australorientalis* (the ratio bregma – opisthocranion length to neurocranium breadth amounts to 107.9%), the parietal bones are slightly convex, the pedicles are moderately long, slightly compressed anteroposteriorly and somewhat inclined backward. The basioccipitale is bell-shaped, broadened in the pharyngeal tuberosities as in *P. australorientalis* and *P. warthae*. The preserved left

bullae tympani is moderately large, smooth and rounded as in *P. warthae*. Although the first tine is not preserved, one can observe that the first ramification is situated rather high above the burr, though not as high as in *P. australorientalis*. The cross-section of antler base is circular, however, the antler forms a specific anteroposterior extension below the first ramification. The antler beam is cylindrical above the first ramification and extends anteroposteriorly below the second ramification as in *P. lyra*. The side surfaces of the antler are concave in the area of the second ramification. The second tine is somewhat compressed anteroposteriorly, set in the perpendicular plane with respect to the flattened portion of the antler beam and is situated at a long distance from the first tine, much longer than in *P. australorientalis*. The antler beam above the second tine is strongly compressed in the anteroposterior direction and gradually becomes broadened distally. The distalmost part of the antler is not preserved. The perpendicular orientation of the second antler ramification with respect to the plane of the flattened distal part of beam is a variable character in the sample from Olivola. The fragment of right hemimandible IGF1394 from Olivola with molarized P_4 could be ascribed to this cervid form.

Most probably, *Praeelaphus* from Olivola represents a true species, however, this question requires a detailed study, since the fauna from Olivola contains another small-sized cervid *Cervus nestii* (Croitor 2014). The small-sized *Praeelaphus* survived on the Italian peninsula until the “wolf event” faunal turnover and went extinct just before the dispersal of the first primitive *Dama eurygonos* with simple four-tined antlers in the Tasso F. U. (Croitor 2006a). Apparently, the presence of *Praeelaphus* in the Early Pleistocene of the Italian Peninsula has a refugial character. Possibly, *Praeelaphus* also survived in the Transcaucasian refugium; at least some cervid remains from the Early Pleistocene fauna of Dmanisi (Georgia) may be ascribed to this genus (Croitor 2017).

Genus *Arvernoceros* Heintz, 1970

Arvernoceros was for the long time considered as an endemic monotypic cervid genus from the Early Villafranchian of Western Europe. The phylogenetical affinity and systematical position of *Arvernoceros* have been discussed for many decades. Teilhard de Chardin & Piveteau (1930) supposed that *A. ardei* is closely related to modern *Elaphurus*. Lister (1987) regards *Arvernoceros* as a genus *incertae sedis*. Vislobokova (1990, 2012) followed Heintz’s (1970) hypothesis on phylogenetic relationship between *Arvernoceros* and *Megaloceros*, and included *Arvernoceros* in the tribe Megacerini. Di Stefano & Petronio (2002) suggested that *Arvernoceros ardei* is closely related to *Axis shansius*, and included *Arvernoceros* in the synonymy of *Axis*. Apparently, this point of view is entirely based on the plesiomorphic for Cervinae three-pointed bauplan of antlers shared by *Arvernoceros* and *Axis*. However, *A. ardei* is more primitive than *Axis* in long and parallel pedicles, while antlers of *A. ardei* are more specialized in frequent development of distal palmation with three crown tines. Such a mosaic combination of advanced and primitive characters suggest that the phyletic relationship between *Axis shansius* and *Arvernoceros ardei* is impossible.

Apparently, the extinct genus *Arvernoceros* is phylogenetically close to modern *Rucervus*. The pattern of antler construction of *A. ardei* corresponds to modern *Rucervus duvaucelli*, which evolves antlers with the dichotomous pattern of the distal crown ramification. The basal tine of *Rucervus duvaucelli* is often supplemented with an additional small prong. According to the genetic studies carried out by Pitra et al. (2004), the modern genus *Rucervus* together with *Axis* is a Late Miocene off-shoot of the Cervinae phylogenetical stock. Therefore, *Rucervus*, likely, is a part of the early radiation of Cervinae that produced Early Pliocene *A. ardei*. It is difficult to assume if *Arvernoceros* and *Rucervus* are synonymous or not, since the shape of antlers is a rather unsafe criterion at the genus level. The definitive conclusion may be obtained from the detailed comparative study of cranial morphology of *Arvernoceros* and *Rucervus*. *Arvernoceros* also shows some affinities with *Panolia*, which superficially resembles *Rucervus*, but is close to *Cervus*. Both *Panolia* and *Cervus* are characterized by narrow triangular basioccipitale, unlike *Rucervus* and *Arvernoceros*. The systematic and diagnostic significance of the shape of basioccipitale is not clear yet, but according to my observations the narrow triangular shape of basioccipitale is characteristic of *Muntiacus muntjak*, *Cervus elaphus* and phylogenetically allied with *Cervus* modern species (*Rusa unicolor*, *Panolia eldi*).

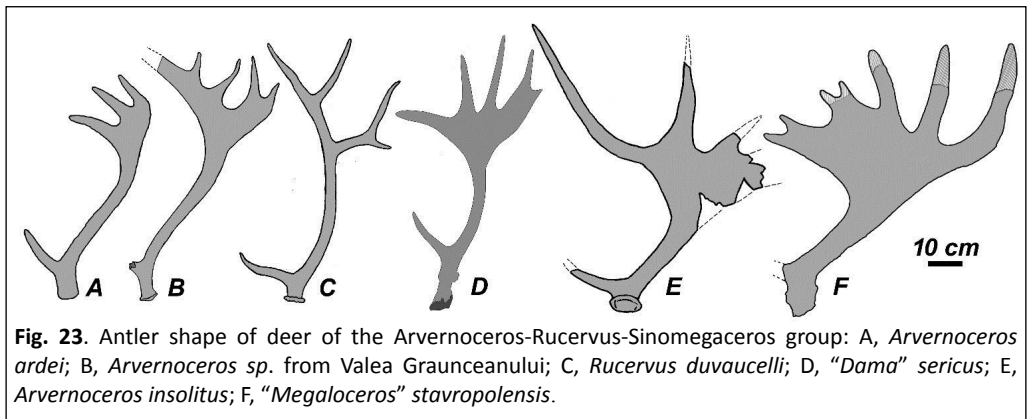


Fig. 23. Antler shape of deer of the Arvernoceros-Rucervus-Sinomegaceros group: A, *Arvernoceros ardei*; B, *Arvernoceros* sp. from Valea Graunceanului; C, *Rucervus duvaucelli*; D, "*Dama*" *sericus*; E, *Arvernoceros insolitus*; F, "*Megaloceros*" *stavropolensis*.

ARVERNOCEROS ARDEI (CROIZET & JOBERT, 1828)

This is a rather large deer with the estimated body mass amounting to ca. 180 kg. The general bauplan of its antlers is simple: the first basal tine is situated high above the burr, may be somewhat flattened and supplemented with a small accessory prong; the antler beam with circular cross-section is terminated with a small distal fork, which in mature specimens is extended into a small terminal palmation (Fig. 23, A). Heintz (1970) ascribed to *Arvernoceros ardei* upper cheek teeth with cingula, assuming that the flattened basal tine and upper molars with cingula prove its direct phyletic relationship with *Megaloceros giganteus*. Heintz (1970) could not associate the antlers from Perrier-Etouaires (France) with lower mandibles, since the sample of fossils represents a mixture of remains of two equally sized cervids *A. ardei* and *Praeclaphus perrieri*. Nonetheless, as it was already assumed here, *A. ardei* is characterized by

simple unmolarized P_4 and relatively long series of lower premolars. A complete well preserved cranial material of *A. ardei* is missing. The available skull fragments bring to us the following characters: pedicles are rather long, strong and cylinder-shaped, the profile of frontal bones is convex between pedicles, the profile of parietal bones is slightly concave, and the basioccipitale is broad, extended in the area of pharyngeal tuberosities (bell-shaped).

This deer is characterized by a mixture of primitive features (the long parallel pedicles trended backwards; the simple antler plan corresponding to three-pointed evolutionary stage; primitive dentition with simple P_4 and relatively long premolar series) and such advanced characters as the large body size and the distal antler palmation in mature males. The shape of distal palmation of the type specimen with three tines pointed forwards, possibly, is not typical. The distal fragment of antler PET1024 from Perrier (NMNH) suggests that the palmation was bilobed, with two prongs on the one of the preserved lobe of palmation stemmed from the posterior side of the main beam, and, apparently, evolved from a simple distal fork.

Rucervus sivalensis (Lydekker, 1880) from Sivaliks represents a special interest for the present discussion. This is a medium-sized deer (ca. 230 kg), based on a single isolated molar with a clearly developed lingual cingulum Lydekker (1885: p. 105, fig. 10). Lydekker (1885) assumed its close relationship with modern *Rucervus duvaucelli* and included it in the arbitrary "Rucervine group". Lydekker (1885) also mentioned a cranium and antler fragments that show a certain resemblance to modern *Rucervus*. This material is discussed in more details by Azzaroli (1954). Colbert (1935) confirms the resemblance of antlers and skull Nr. 19829 (American Museum of Natural History) of "*Cervus*" *sivalensis* with *R. duvaucelli*. The length of the lower molar series M_1 - M_3 amounts to 78.0 mm (Colbert 1935), representing an intermediary value between the range of lower molar series length of *perrieri/ardei* sample from Perrier (68.4-72.8 mm, $n = 5$) and *Arvernoceros sp.* from Liventsovka (Baygusheva 1994), South Russia (Nr. 1810/3 = 90.0 mm; Nr. КП-1785/144 = 87.7 mm; Nr. MK-1419/2 = 91.9 mm; RSU). The antler is heavily build, with a round cross-section; its crown is formed by at least three crown tines inserted on the posterior side of the distal part of the beam (Colbert 1935: fig. 146) as in modern *Rucervus duvaucelli*. This shape of antler known strikingly reminds the distal portion of *A. ardei*. In my opinion, a close phylogenetic relationship between *A. ardei* and *R. sivalensis* seems to be more than probable. *Pseudalces mirandus* Flerov, 1962 could stand even closer to *R. sivalensis*: the length of the upper molar series of *Pseudalces* is 77 mm (measured from fig. 3C in Vislobokova 1986), thus standing very close to the specimen described by Colbert (1935). Upper molars of *Pseudalces* are supplemented with large entostyles that attain the greatest development in M^3 and may be regarded as a sort of cingulum.

A. ardei was reported by Heintz (1970) from several Lower Villafranchian sites of France and Spain. The earliest record of *Arvernoceros* in Europe was reported from the Late Ruscinian (Early Pliocene) of Węże-1 (Poland); this is a frontal part of skull, which morphologically corresponds to the frontal shape of *A. ardei* from Perrier-Etouaires

(Croitor & Stefaniak 2009). A few remains from Pliocene site Węże-2 (Poland) ascribed to *Arvernoceros* (Stefaniak 1995), in fact, are poor and their systematical determination remains arbitrary. The shed antler from the Villafranchian deposits of Slobozia Mare (Moldova) extends the area of distribution of *A. ardei* to southeastern Europe (Croitor 2009).

ARVERNOCEROS VERESTCHAGINI DAVID, 1992

This is a very large species with rather simple shape of antlers. The holotype, a single known antler from the Villafranchian of Salcia (Moldova), is similar in general bauplan to *A. ardei*, but is significantly larger (the diameter of antler base is ca. 10 cm), and lacks distal palmation (David 1992). The antler ends with a simple distal fork. The basal tine is strong, extended into a small palmation with three prongs. Possibly, *A. verestchagini* is closely related to "*Cervus*" *colberti* AZZAROLI, 1954, which is based on the damaged skull Nr. 19829 (AMNH). "*C.*" *colberti* shares with *Rucervus sivalensis* the presence of a weak lingual cingulum in the upper molars, but is somewhat larger (360 kg) than the latter species. The length of the upper molar series amounts to ca. 82.0 mm (measured from the fig. 145 in Colbert 1935), approaching to the lower range of the size variation of *Megaloceros giganteus* (NHML, n = 11). AZZAROLI (1954) distinguishes "*Cervus*" *colberti* from *Rucervus sivalensis* by its weaker cingulum and more rounded "inner crescents" (apparently, protocone and hypocone). The degree of cingulum expression may be an individually variable character, while the lingual outlines of protocone and hypocone depend of the stage of molar wear, which seems to be very advanced in the type specimen (COLBERT 1935: fig. 145). Therefore, there is a high probability that "*Cervus*" *colberti* AZZAROLI, 1954 is an advanced form closely related to *Rucervus sivalensis* (LYDEKKER, 1880).

ARVERNOCEROS CF. *VERESTCHAGINI* FROM APOLLONIA

The extremely large cervid (ca. 700 kg) from the Late Villafranchian of Apollonia (Greece) possibly is an advanced descent of "*Cervus*" *colberti*. The sample from Apollonia was originally regarded as a single giant form with some peculiar characters referred to as *Megaloceros* sp. (Kostopoulos 1997). Later on, van der Made (1999) ascribed the remains of the large-sized deer from Apollonia *Eucladoceros giulii* Kahlke 1997. The subsequent revision of the large cervid material from Apollonia revealed the presence of *Praemegaceros pliotarandoides* and another giant deer similar to *A. verestchagini* (Croitor & Kostopoulos 2004). The basal fragment of the right antler

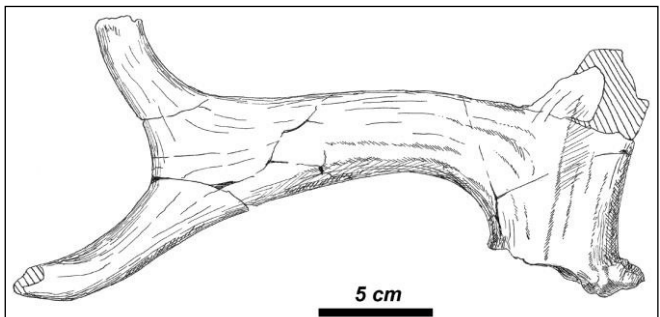


Fig. 24. The basal fragment of the right antler APL-357 (GSUT) of *Arvernoceros* cf. *verestchagini* from the Early Pleistocene of Apollonia-1, Greece.

APL-357 (GSUT, Fig. 24) has a first tine directed towards to the anterior, springing off the beam at a certain distance from the burr and forming an oblique angle with the beam ($\sim 110^\circ$). The distal part of the first tine becomes gradually broadened and flattened, ending with two prongs diverging under the almost right angle. The first tine broadening is oriented in the vertical plane, unlike the horizontal orientation of the first tine flattening in *M. giganteus*.

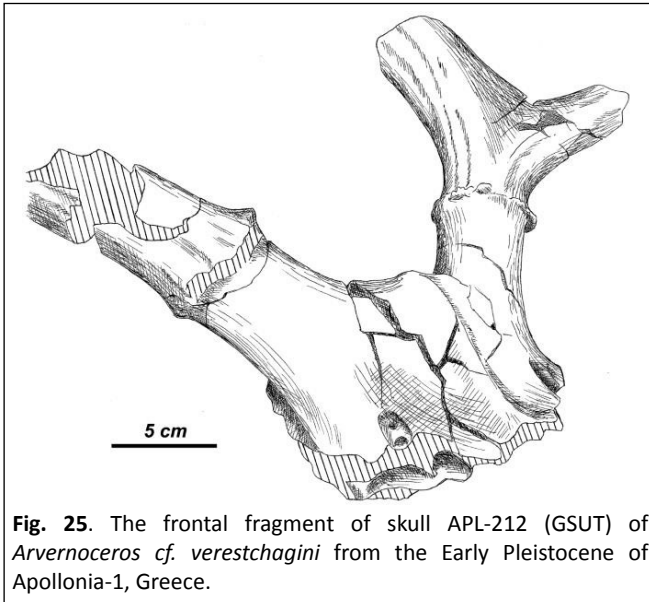


Fig. 25. The frontal fragment of skull APL-212 (GSUT) of *Arvernoceros cf. verestchagini* from the Early Pleistocene of Apollonia-1, Greece.

The frontal fragment of skull APL-212 (GSUT, Fig. 25) preserves the proximal parts of the antlers. Its breadth at frontal constriction is 168.7 mm, the breadth of braincase behind pedicles is 122.7 mm. The first tine has a higher position than in the previous specimen. The first bifurcation height amounts to 133 mm. The antler base is more or less circular but the antler is strongly compressed lateromedially in the region of first branch. At the base of the first tine, the antler surface is

depressed. The beam transversal cross-section is regularly circular above the first branch. The frontal bones have a very prominent lateral profile between the pedicels and slightly concave before the pedicels. In the anterior view, the interfrontal region is flat. The frontal bones on the sides of the interfrontal suture are somewhat depressed and concave in the supraorbital region. The pedicles are very long for a deer of such a large size, strong and cylindrical, pointed somewhat sideward and backward, so they are situated in the plane of frontal bones, forming a right angle of divergence. Unlike deer of the genus *Praemegaceros*, a bony ridge does not border the medial side of the pedicle bases. The skull frontlet from Apollonia is somewhat broader and has the longer pedicles if compared to *Arvernoceros sp.* from Liventsovka (ca. 300 kg; breadth of frontal constriction is 123.4 mm; breadth behind pedicles is 96.3 mm) described by Baygusheva (1994). The frontals are more flattened between the pedicles and orbits, unlike the deeply depressed frontals of the specimen from Liventsovka. The antler shape of the specimens from Apollonia and Liventsovka display a great similarity, although the Apollonian form is larger with longer pedicles. Possibly, the long pedicles of the Apollonia frontlet suggest that the specimen belongs to a younger individual.

The lingual side of P^2 is split, so protocone and hypocone are clearly separated from each other (Croitor & Kostopoulos 2004). The enamel of interior side of the hypocone is folded, forming together with the metacone an enamel islet. The lingual slope of P^3 is

grooved; however, the protocone and the hypocone are not separated. The enamel of the interior side of the hypocone is folded. A small isolated enamel islet is present in the hypocone. The lingual slope of P⁴ has a shallow groove. The enamel of the interior side of the hypocone is folded as well. Upper molars are supplemented with an entostyle and a hypoconal spur. A small but clearly expressed cingulum is present in one M³, as in "*C.*" *colberti* and *R. sivalensis*.

The left ramus of mandible APL-384 belongs to a very large deer of comparable size to *M. giganteus*. The specimen from Apollonia does not display the mandibular pachyostosis, so characteristic of the Irish giant deer (Croitor & Kostopoulos 2004). P₃ is of simple morphology and its metaconid has a slightly broadened antero-posteriorly distal end. The parastylid and paraconid of P₃ are connected, closing a small enamel islet. P₄ is not molarized. The parastylid and paraconid of P₄ also close an enamel islet. The lingual part of the metaconid extends antero-posteriorly but it does not fuse with the paraconid or the entoconid, even in advanced stage of wear (APL-33). The entoconid is sloped backwards and get in touch with entostylid, without however to be fused together. Lower molars are supplemented with well-developed ectostylids.

The metapodials are extremely long and relatively much longer if compared to the fossil deer of the similar body weight class. Metacarpal bones of the Apollonian deer are almost of the same length as metatarsals and radius. These unusual for such a large deer limb proportions are regarded as an adaptation to high-lever feeding on the tree-crown leaves, occupying an ecological niche more or less similar to that of modern giraffes (Croitor & Kostopoulos 2004).

ARVERNOCEROS GIULII (KAHLKE, 1997)

The peculiar long-limbed large-sized (ca. 385 kg) cervid from the end of Early Pleistocene of Untermassfeld (Germany) was described by Kahlke (1997) as the new species *Eucladoceros giulii*. Kahlke (1997) and van der Made (1998, 1999) ascribed this deer all the late Villafranchian deer from Spain (Atapuerca, Venta Micena), Germany (Würzburg-Schalksberg), Greece (Apollonia) and Georgia (Akhalkalaki) based on the extremely large size of postcranial bones. In the opinion of van der Made (1998, 1999), the size and morphology of metapodials are of particular interest for the systematics of the large Pleistocene deer. Nonetheless, any attempts to involve the morphology, proportions and size of appendicular skeleton in the systematic research are quite delicate, since all ectosomatic organs are strongly influenced by ecological conditions, highly variable and may also depend on landscape character, climate conditions, body weight and species ecology (Köhler 1993; Croitor & Kostopoulos 2004). Apparently, the sample of large-sized cervids from Untermassfeld includes two distinct taxa: a long-limbed cervid similar to *Arvernoceros/Rucervus* lineage and the more robust form similar to *Praemegaceros plotarandoides* (Croitor & Kostopoulos 2004).

Since the species definition is based only on the extremely large and long limb bones, it makes some difficulties in distinguishing this deer from the deer of the genus *Eucladoceros*, the diagnoses of which are based on the antler morphology. The

complete antlers of *Arvernoceros giulii* are not known. The hypothetical reconstruction of the antler is based on scant fossil fragments (Kahlke 1997: fig. 28) belonging to individuals of different ontogenetic ages and therefore the eucladocerine comb-like structure provided is not fully supported. In fact, the juvenile antler IQW 1990/23 from Untermassfeld belongs to a skull specimen illustrated lately by Kahlke (2001: pl. 74, fig. 1). Both the antler and skull morphology show a certain affinity to the antler type of *Arvernoceros*, as well as to the frontlet from Apollonia: the interfrontal region is wide and flat, the frontals are slightly concave in front of the pedicels, the interfrontal suture is slightly raised, the pedicels are very long and cylindrical, pointed sideward and backward and diverged almost vertically, the flattened first tine is situated very high and forms a terminal fork with vertical orientation as in the specimen APL-357 from Apollonia. The distal part of the antler is somewhat flattened and dichotomously divided in two branches following the *A. verestchagini* condition. The juvenile antler from Untermassfeld figured by Kahlke (1997: 229, fig. 26) does not recall any ontogenetic stage of the antler development in a comb-antlered *Eucladoceros* that is displayed by the sample from Peyrolles (Bout & Azzaroli 1952). Moreover, the dental morphology of *A. giulii* is quite different if compared to typical eucladocerines: the lingual surfaces of upper premolars are not cleft nor grooved and the lower premolar row is relatively long if compared to the sample of *E. ctenoides* from Ceyssaguet (Croitor & Kostopoulos 2004). Taking into account all these arguments, Croitor & Kostopoulos (2004) consider that the large-sized deer from Untermassfeld with long metapodials, simple morphology of P_4 and high-positioned flat and branched first antler tine should be ascribed to the genus *Arvernoceros* as *Arvernoceros giulii* (Kahlke, 1997).

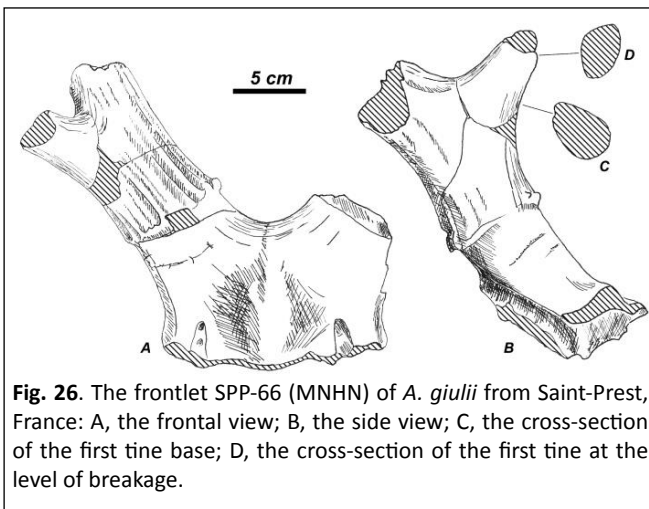


Fig. 26. The frontlet SPP-66 (MNHN) of *A. giulii* from Saint-Prest, France: A, the frontal view; B, the side view; C, the cross-section of the first tine base; D, the cross-section of the first tine at the level of breakage.

A similar to *A. giulii* deer from Saint-Prest, France (MNQ20, ca. 1.0 Ma) was reported as *Praemegaceros verticornis* (Guerin et al. 2003). The frontlet SPP-66 (MNHN, Fig. 26) from Saint-Prest with proximal fragment of right antler belongs to a large-sized deer with the frontal breadth amounting to 157.4 mm. The breadth of braincase behind pedicles is 112.0 mm. Unlike *P. verticornis*, the specimen SPP-66 is characterized

by the concave frontal bones, the circular cross-section of pedicles (DLM×DAP $dx = 75.0 \times 66.8$ mm), the absence of bony burelets bordering the pedicle base from median side, and the oval cross-section of the first tine situated on the anterior side of the antler beam. The mandible SPR-73 (dx) is characterized by the primitive unmolarized P_4 with a small enamel istlet between parastylid and paraconid as in the large deer from Apollonia. The horizontal ramus of mandible is rather robust, but I cannot say that it

is affected by pachyostosis. The same deer is known from Rosieres (France) as *Cervus (Megaceros) dupuisi* Stehlin, 1912.

Here should be also mentioned the large-sized deer from the Late Villafranchian fauna of the Vallonnet Cave (South France) reported as *Praemegaceros cf. verticornis* (Mouille et al. 2006). The deer from Vallonnet is characterized by the simple P_4 , the vestigial cingulum in upper molars, and the small protoconal fold observable in little worn molars. Antlers are robust (DAP of antler base in specimens Nr. 132 and Nr. 368, RMPM, is 69.6 mm and 65.0 mm correspondingly) characterized by the high position of basal tine (101.3 mm in the specimen Nr. 132), and the strong bending of the beam toward the posterior at the level of the first ramification.

ARVERNOCEROS INSOLITUS VEKUA, BENDUKIDZE & KILADZE, 2010

A new large-sized form of deer with palmated antlers was described from the Early Pleistocene of Dmanisi (Georgia). The holotype is a shed antler characterized by very long terminal tines and a palmation that apparently is supplemented with several posterior smaller crown tines (Fig. 23, E). The basal tine is situated very close to the burr (Vekua et al. 2010). The antler bauplan reminds "*Dama*" *sericus* Teilhard de Chardin & Trassaert, 1937 (Fig. 23, D), a much smaller deer from Pliocene of Shansi (China).

ARVERNOCEROS STAVROPOLENSIS (TITOV & SHVYREVA, 2016)

This medium-sized species (DLM above burr amounts to 60.7 mm) from the Early Pleistocene (Late Villafranchian) of Ciscaucasia is very close to the previous one, but is distinguished by the higher position of the basal tine, the short terminal tines and the stronger development of palmation with massive posterior tines (Fig. 23, F). The antler beam cross-section is subtriangular, unlike *A. ardei* and *A. verestchagini* characterized by the circular beam cross-section. Titov & Shvyreva (2016) regard the species in question as a transitional form between *A. ardei* and *Megaloceros giganteus*. Actually, the antler shape of *A. starvopolensis* shows a great affinity with "*Dama*" *sericus*, while the resemblance with *M. giganteus* is rather superficial.

ARVERNOCEROS SP. 1 FROM VALEA GRAUNCEANULUI

This rather large deer (230 kg) from the Early Pleistocene of Valea Graunceanului (Romania) was reported as *Eucladoceros sp.* by Radulesco et al. (2003) and as *Arvernoceros sp.* by Croitor (2009), and its systematic position is still uncertain. The fossil material includes fine fragments of antlers, some cranial remains, mandibles and the large number of postcranial bones. The almost complete antler Gr965-c.17-690 (ISB) is characterized by a high position of the first ramification above burr (106.2 mm) and a gently curved beam terminated with a broad palmation (Fig. 23, B). The length of the antler amounts to 540 mm. The DAP of antler base is 43.3 mm. The distal antler fragment Gr965-c.17-720 (ISB) has a bilobed palmation terminated with at list five distally oriented tines. The general structure of the antlers from Valea Graunceanului reminds *Rucervus duvaucelli* (Croitor 2009). A badly damaged female skull from Valea Graunceanului (ISB, no number) shows that nasal bones were rather short and did

not reach the line connecting the anterior edge of orbits. The anterior edge of orbit is situated above M^3 . The basioccipitale is broad in pharyngeal tuberosities, bell-shaped. The length of right upper tooth row amounts to 130.0 mm (L P^2P^4 – 58.8 mm, L M^1M^3 – 77.2 mm); the breadth of occipital condyles amounts to 72.3 mm; the palatal width between M^3 amounts to 70.7 mm. Upper molars have no cingulum and no protoconal enamel fold. The splanchnocranial fragment Gr963-c.b6-n.II-277 of an old individual is poorly preserved, but is very interesting, since it shows the presence of an alveolus of upper canine. The lower premolar series is relatively long (premolar to molar series length ratio varies between 64.7 and 72.5 mm, $n=9$). P_4 is primitive non-molarized; its parastylid and paraconid are separated; metaconid is rounded and somewhat extended anteroposteriorly.

The cranial and dental morphology of the deer from Valea Graunceanului is very similar to that of *Rucervus simplicidens* (Lydekker, 1876) from Sivaliks. *R. simplicidens* is distinguished from other rucervine deer of Sivaliks by the absence of cingulum in the molars and more hypsodont teeth. The cranium BM39570 reported by Azzaroli (1954) as *Rucervus cf. simplicidens* is characterized by the presence of small upper canines; the large ethmoidal openings with a long border formed by the nasal bones at more than $\frac{1}{2}$ of ethmoidal opening length; and the anterior edges of the orbits

situated above the posterior edge of M_3 . The enlisted characters approach *R. simplicidens* to modern *R. duvaucelli*. Unlike modern barasingha deer, *Rucervus* from the Sivaliks and the deer from Valea Graunceanului are characterized by short nasal bones that do not reach the line connecting the anterior edges of the orbits that represents a primitive ancestral character. The deer from Valea Graunceanului is somewhat larger than *R. simplicidens*, which attained 170 kg of body mass (Croitor 2017). The final conclusion on taxonomical status and systematical position of the deer from Valea Graunceanului should be done in the context of a revision of fossil material from Europe and Sivalik Hills ascribed to the genera *Arvernoceros* and *Rucervus*.

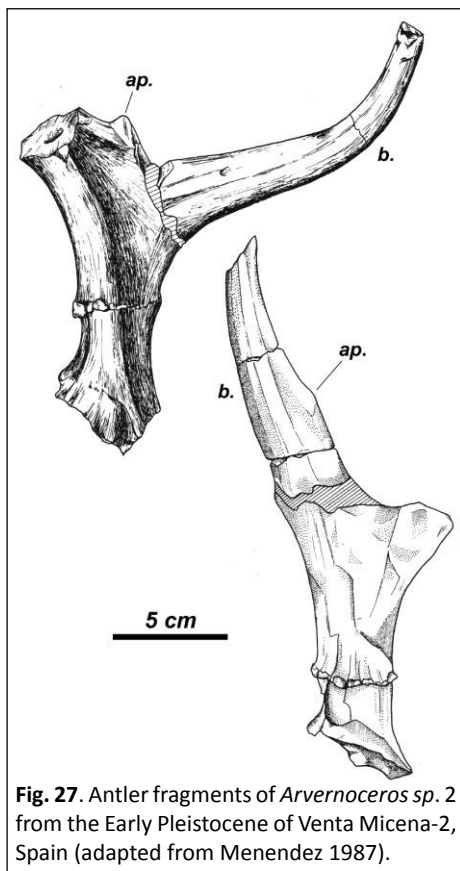


Fig. 27. Antler fragments of *Arvernoceros* sp. 2 from the Early Pleistocene of Venta Micena-2, Spain (adapted from Menendez 1987).

ARVERNOCEROS SP. 2 FROM VENTA MICENA-2

Menendez (1987) described remains of a medium-sized deer from the Early Pleistocene of Venta Micena-2 (Spain) as "*Cervus*" *elaphoides*. According to Lister (1990), the small-sized cervid from Venta Micena is a genuine and undescribed yet species.

The fossil material from Venta Micena is quite poor and includes only fragmentary remains of antlers, upper and lower dentition, and limb bones. The antlers figured by Menedez (1987) are characterized by the high position of the first ramification (height of ramification is 2-3 times larger than the diameter of antler base), the somewhat compressed lateromedially proximal part of the basal tine, and the accessory prong, which in one case is situated on the basal tine, and in another case is located in the area of the basal ramification (Fig. 27). The antler beam is curved toward the posterior immediately above the basal ramification. The pedicles are moderately long. The enlisted antler characters approach the cervid under discussion to *Arvernoceros ardei*, however, the deer from Venta Micena is somewhat smaller: the length of upper tooth row of *A. ardei*, according to Heintz (1970), varies between 97.5 and 109.0 (n=4), while length of upper cheek teeth in the deer from Venta Micena ranges from 81.3 to 84.1 mm (n=4) (Menendez 1987). The dental morphology of the deer from Venta Micena is more advanced if compared to *A. ardei*: P_{4^*} is variable and in some cases is molarized; the upper premolar row is relatively short (the upper premolar to molar series ratio amounts to 65.8% in the sample from Venta Micena and to 78.8% and 73.9% in the samples with *A. ardei* conform the data of Heintz 1970); the lingual cingulum in upper molars is reduced, however, the entostyle is large, flattened, and strong. The cervid from Venta Micena and *A. ardei* are characterized by the similar morphology of upper premolars: the hypocon and the protocon of P^2 and P^3 are separated, the anterior wing of the hypocon of the upper premolars is supplemented with an additional enamel fold (Heintz 1970: pl. XXXIV; Menéndez 1987: 175, pl. 2, fig. 3). Therefore, the small cervid from Venta-Micena is closely related to *A. ardei*, but distinguished by somewhat smaller size and more advanced morphology of dentition.

Genus *Haploidoceros* Croitor, Bonifay & Brugal, 2008

Bonifay (1967) described few fragments of robust antlers of a medium-sized deer from the Middle Pleistocene deposits (Mindel-Riss Interglacial, ca. 0.30-0.35) of Lunel-Viel (Southern France) as *Euctenoceros mediterraneus*. The subsequently discovered new fossil material revealed an advanced evolutionary specialization of cranial, dental, and antler morphology that permitted us to create a new monotypic genus *Haploidoceros*.

HAPLOIDOCEROS MEDITERRANEUS (BONIFAY, 1967)

Large, massive, but simple antlers represent the most remarkable feature of this species. The robust fully grown antlers have only two points: the long sickle-shaped beam and the strong basal tine. The shed antler LV-IV-15728 (MNP) is the most complete specimen, preserving the main beam (Fig. 28). The antler beam is very long (907 mm) and has almost the same diameter as the basal tine. Right above the bifurcation, it bends backwards and sideways, then the antler curves uprights, and its distal portion is pointed forward. The transverse cross-section of the antler beam is mainly circular; the distal portion of the antler is slightly compressed mediolaterally. The basal tine is inserted high above the burr and is oriented along the axis of the antler base and pedicle. The base of tine is somewhat compressed in the lateromedial direction. The distal portion of the tine has a regular circular cross-section. The individual variation

of the antlers concerns the angle of the basal ramification, which varies in the sample from Lunel-Viel from 60° to 80°.

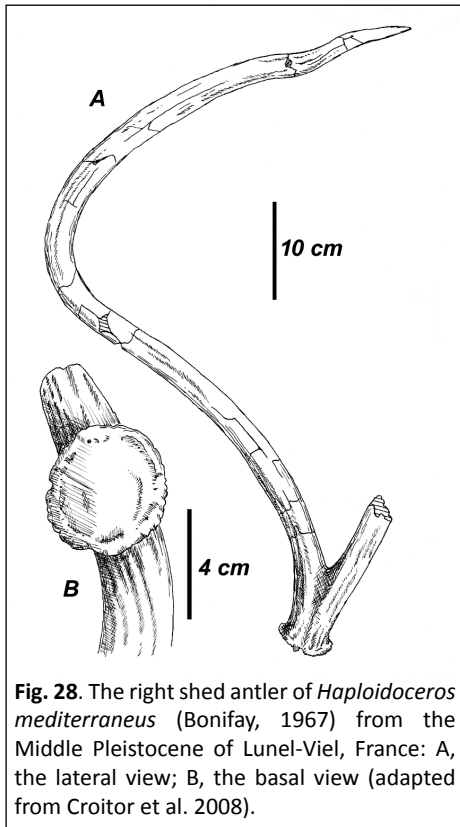


Fig. 28. The right shed antler of *Haploidoceros mediterraneus* (Bonifay, 1967) from the Middle Pleistocene of Lunel-Viel, France: A, the lateral view; B, the basal view (adapted from Croitor et al. 2008).

The pedicles are very short and robust, sloped backwards and sideward. The extremely short and robust pedicles in *H. mediterraneus* represent another remarkable distinctive character of this cervid. The pedicle height measured from the postero-medial side is approximately 1/3 of the pedicle diameter. The transverse cross-section of the pedicles has a regular circular shape. The neurocranium LV-IV-14911 (MNP) from Lunel-Viel is elongated, unflexed, with slightly convex parietal and temporal bones. The body of the basioccipitale is broad and bell-shaped. The *foramina ovale* are small, with an irregular rounded shape. The *bullae tympani* are large, rounded, somewhat compressed laterally, prominent, with a rib and a rostral bony thorn. The occipital is comparatively low, with well-developed and prominent crests and ridges for nuchal muscles. The frontal bones are very broad (the estimated breadth is 120 mm) with respect to the braincase breadth. Apparently, the relatively broad frontals of *H. mediterraneus* is correlated

with the sideward orientation of pedicles. The modern species *Rucervus duvaucelli* shows the greatest affinity in the proportions of the neurocranium with the skull from Lunel-Viel (Croitor & al. 2008).

The premolar series is comparatively short. The lingual wall of P² is cleft, so the hypocone and the protocone of P² are separated. The anterior wing of the hypocon has an internal enamel fold. The hypocone and the protocone of P³ are separated as well. The anterior wing of hypocone is supplemented with a large enamel fold projecting inward and backward. The lingual wall of P³ may be cleft (5 cases out of 21). The upper molars are characterized by the presence of an entostyle and a hypoconal spur (eperon). Only rudimentary remains of a cingulum are observed in M² and M³ of some specimens. P₄ is always molarized. The upper and lower premolar series are relatively short.

The evolution of *H. mediterraneus* took place in the Iberian glacial refugium during the early Middle Pleistocene. *Arvernoceros sp.* from the Early Pleistocene of Venta Micena-2 is the direct forerunner of *H. mediterraneus* that developed toward the molarization of P₄, the relative shortening of upper and lower premolar series, the simplification of antlers. Pedicles became shorter and more divergent. Among the characters that indicate the phylogenetic relationship between *Arvernoceros ardei* and

Haploidoceros mediterraneus we can mention the high position of basal ramification, the bending of beam toward the posterior immediately above the basal ramification, the compressed proximal part of the basal tine that reminds the flattened basal tined in *Arvernoceros*, the circular cross-section of the antler beam, and the cleft lingual walls in upper premolars. The weak flattening of the distal part of the beam observed in the specimen LV-IV-15728 may be interpreted as a vestige of distal palmation of *Arvernoceros*.

Abundant remains of *H. mediterraneus* were also reported from the Late Pleistocene of Cova Del Rinoceront, Iberian Peninsula (Sanz et al. 2014), thus confirming the importance of the Iberian glacial refugium for evolution of this endemic cervid. The Iberian material shows essentially the same morphology as the sample from the type locality.

Genus *Eucladoceros* Falconer 1868

The name *Eucladoceros* was created as a subgenus of the genus *Cervus* containing the fossil cervid species *Cervus (Eucladoceros) sedgwickii* (Falconer 1868: 472) from Bacton, Norfolk (England). Simpson (1945) elevated *Eucladoceros* Falconer to the genus rank and included *Polycladus* Pomel 1854 in the synonymy of Falconer's genus. Azzaroli (1947, 1953) considered the use of Falconer's *Eucladoceros* objectionable because of the confusing homonymy with *Cervus (Rusa) eucladoceros* Falconer, 1868 (a synonym of *Rucervus duvaucelli*), but this is not the case. Azzaroli (1947, 1953) proposed to substitute *Eucladoceros* Falconer with *Euctenoceros* Trouessart, 1898 with the type species *Cervus tetraceros* Dawkins, 1875, but this taxonomic procedure was not supported. *Eucladoceros* is easily recognizable by its peculiar comb-like antlers (Fig. 29). The phylogenetical relationships of *Eucladoceros* remained unclear.

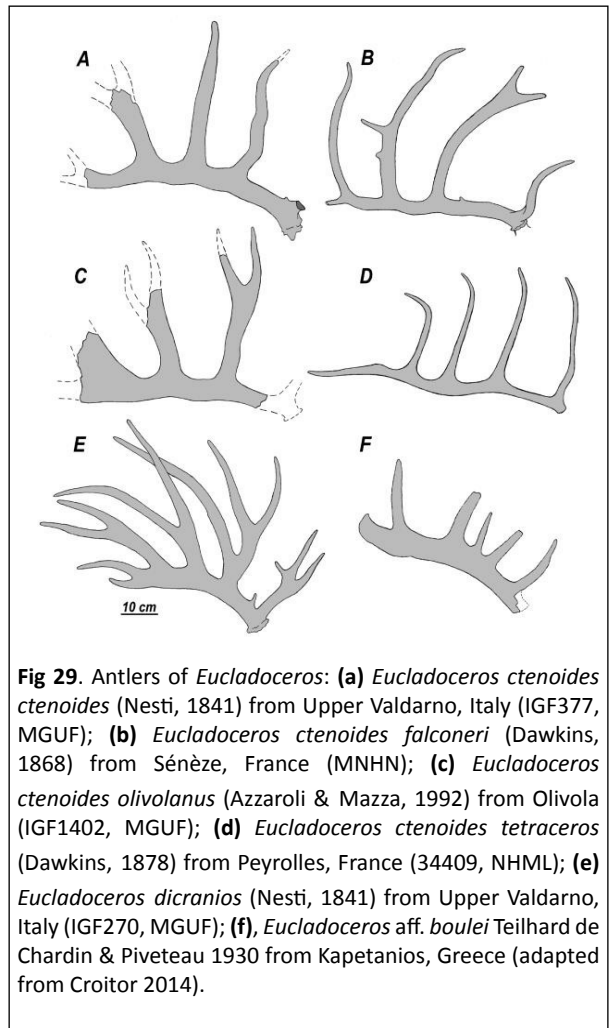


Fig 29. Antlers of *Eucladoceros*: (a) *Eucladoceros ctenoides ctenoides* (Nesti, 1841) from Upper Valdarno, Italy (IGF377, MGUF); (b) *Eucladoceros ctenoides falconeri* (Dawkins, 1868) from S n ze, France (MNHN); (c) *Eucladoceros ctenoides olivolanus* (Azzaroli & Mazza, 1992) from Olivola (IGF1402, MGUF); (d) *Eucladoceros ctenoides tetraceros* (Dawkins, 1878) from Peyrolles, France (34409, NHML); (e) *Eucladoceros dicranios* (Nesti, 1841) from Upper Valdarno, Italy (IGF270, MGUF); (f), *Eucladoceros* aff. *boulei* Teilhard de Chardin & Piveteau 1930 from Kapetanios, Greece (adapted from Croitor 2014).

Flerov (1952: 13) regarded *Eucladoceros* as a forerunner of large-sized Quaternary cervid genera *Megaloceros*, *Cervalces* and *Alces*. The antler morphology of *E. ctenoides* reminds to a certain extent the antlers of modern *Przewalskium albirostris*. I cautioned that the similarity in antler shape between *Eucladoceros* and *Przewalskium* may be superficial and in this case the belonging of *Eucladoceros* to the lineage *Przewalskium-Rusa-Cervus* is improbable (Croitor 2014). However, the results of the analysis of body labyrinth morphology revealed a close affinity between *E. ctenoides* and *C. elaphus*. The results of Mennecart et al. (2017) may suggest that the observed similarity of the comb-like antler shape of *Eucladoceros* and modern *Przewalskium* is not superficial and supports the close relationship between these genera.

EUCLADOCEROS DICRANIOS (NESTI, 1841).

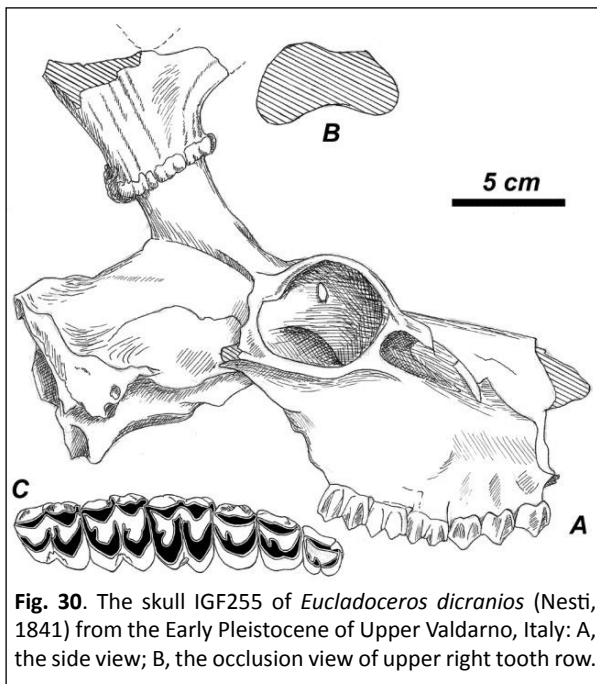


Fig. 30. The skull IGF255 of *Eucladoceros dicranios* (Nesti, 1841) from the Early Pleistocene of Upper Valdarno, Italy: A, the side view; B, the occlusion view of upper right tooth row.

This is the most advanced and possibly the largest (300 kg) species of the genus characterized by particularly complicate morphology of antlers. According to Azzaroli (1947) and de Vos et al. (1995), *Eucladoceros sedgwickii* Falconer, 1868 is a junior synonym of *Eucladoceros dicranios* Nesti, 1841, therefore, *E. dicranios* is the type species of the genus. The type specimen comes from the Early Pleistocene of Upper Valdarno (Italy). *Cervus martialis* Gervais, 1849 from Southern France (Gervais 1859: pl. 21, figs. 2-5) is another synonym of *E. dicranios*.

The fine antlered skull IGF270 (MGUF) is the holotype of *E.*

dicranios (Azzaroli & Mazza 1992a: pls. 1, 2). The first tine is situated at a certain distance from the burr; an accessory specific for the genus subulate tine is situated in the area of first ramification some-what medially (it is directed upright on the antlered skull); the three crown tines inserted on the anterior side of the antler beam (Fig. 29, E). The skull is characterized by the well-developed preorbital pits, the large ethmoidal openings with a long contact with nasal bone and flexed braincase if compared to other forms of *Eucladoceros*. The advanced braincase flexion permits to ascribe the damaged skull IGF255 (MGUF) from Upper Valdarno to *E. dicranios* (Fig. 30). The antler beam and the tines (with exception of the accessory subulate tine) are pronouncedly compressed from the sides. The antler tines are bifurcated or trifurcated, so the right antler has 14 points, while the left one has 12 points (De Vos et al. 1995). The bifurcation of antler tines in *E. dicranios* represents a sort of hypermorphism, which is strongly expressed

in the proximal tines: the first (brow) tine and the first crown tine are flattened and trifurcated. The trifurcation of the first crown tine on each antler resulted from the subsequent bifurcation of the anterior branch of the tine. The second crown tine splits into a bifurcation in its proximal part and forms two very long ramifications. The anterior ramification on the right antler is supplemented with an accessory short prong. The third crown tine forms a smaller bifurcation in its distal portion. The posterior tine of right antler is also bifurcated. The crown tines are deflected somewhat backward. The antler beams are curved sideward therefore the antlers give a peculiar “brushy” impression. This optical illusion caused the incorrect description of antler shape as “brush-like” reported, for instance, by Geist (1998), while the taxonomically significant comb pattern of antler construction remained overlooked. *Eucladoceros dicranios* is quite rare in the paleontological record of Europe. Its known area of distribution ranges from the Azov Sea plains in the East to England in the West (De Vos et al. 1995). The findings from Italy, England and Russia display some minor morphological differences one from another (Azzaroli & Mazza 1992; De Vos et al. 1995), however it is impossible to estimate the significance of those differences since we have at our disposal only one complete specimen from each locality. Baygusheva & Titov (2013) described the sample from the Lower Pleistocene (Middle Villafranchian) of Liventsovka (Azov Area, Russia) as a new subspecies *E. dicranios tanaitensis*, which is considered as a direct forerunner of *Praemegaceros pliotarandoides* regarded by authors as *E. orientalis pliotarandoides* (De Alessandri, 1903) and *E. orientalis orientalis* (Radulesco & Samson, 1967). The type specimen of *E. dicranios tanaitensis* is an incomplete right antler (Baygusheva & Titov 2013: fig. 2b-c) with the rather well-preserved first known tine, which is dichotomously branched into four prongs, and the proximal part of the second crown tine. The distal part of the antler is destroyed. This incomplete preservation of the antler from Liventsovka gives a wrong impression of affinity with the dichotomously branched crown tines of *P. pliotarandoides* antlers, which, however, lack such important diagnostic character of *Eucladoceros* as the comb-like bauplan. It is also necessary to indicate that *Cervus pliotarandoides* De Alessandri, 1903 has a priority over *Psecupsoceros orientalis* Radulesco & Samson, 1967.

EUCLADOCEROS CTENOIDES (NESTI, 1841)

This is a less specialized species with simple metameric comb-like antlers possessing four or five tines (the accessory rudimental tine is not counted). The body size (250 kg) is slightly inferior to that of *E. dicranios* from Upper Valdarno. *E. ctenoides* is based on the right antler IGF 377 (MGUF, Fig. 29, A) from the Late Villafranchian of Upper Valdarno and possibly coexisted with *E. dicranios*. For this reason, it is difficult to distinguish mandibles and postcranial remains of those two species from Upper Valdarno. The first tine of *E. ctenoides* antler is situated at a certain distance from the burr, unbranched and cylinder-shaped. A small accessory tine is situated in the area of first ramification on the anteromedial side of the beam. This accessory tine is often preserved as a knob-like vestige. The antler beam is slightly compressed from the sides between the first and the second tine, and became strongly compressed from the sides above the second tine. The crown tines are situated on the anterior side of the beam and form a right angle with the beam. Azzaroli & Mazza (1992) reported that the dichotomous

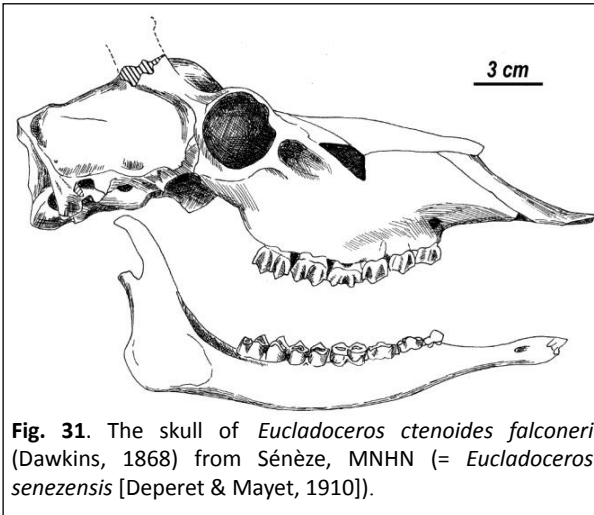


Fig. 31. The skull of *Eucladoceros ctenoides falconeri* (Dawkins, 1868) from S n ze, MNHN (= *Eucladoceros senezensis* [Deperet & Mayet, 1910]).

bifurcation is clearly recognizable on the fourth tine of the holotype of *E. ctenoides*. Apparently, the fifth tine was also dichotomously branched. A similar spontaneous dichotomy of crown tine is observed in the antlered skulls of *Eucladoceros* from S n ze (France) stored in Paris (Fig. 29, B), and some antlers from Olivola (Italy) (Azaroli 1948). Azaroli & Mazza (1992) proposed a new subspecies *Eucladoceros dicranios olivolanus* for the sample from Olivola, which, according to their opinion, represents a mixture

of characters of *E. ctenoides* and *E. dicranios* and was regarded as a forerunner of those two species (Fig. 29, C). The holotype of *E. dicranios olivolanus* is a distal portion of antler IGF1402 with three crown antlers. Azzaroli (1947) originally described this specimen as *Cervus (Euctenoceros) ctenoides*. The two crown tines have their distal parts bifurcated reminding to a certain extent *E. dicranios*. The first tine in *Eucladoceros* from Olivola (seen in other specimens) is cylinder-shaped and unbranched as in *E. ctenoides*. Since the occasional incipient bifurcation in crown tines is characteristic of *Eucladoceros ctenoides*, this unstable crown tine bifurcation, obviously, should be regarded as a hypertrophy, but not a transitional evolutionary stage between *Eucladoceros ctenoides* and *Eucladoceros dicranios*. Therefore, *Eucladoceros dicranios olivolanus* is a junior synonym of *Eucladoceros ctenoides*, or, at list, should be kept as the subspecies *Eucladoceros ctenoides olivolanus*. Unlike the antler hypermorphism in *Eucladoceros dicranios*, the antler hypertrophy in *Eucladoceros ctenoides ctenoides* is stronger expressed in the posterior crown tines.

The skull of *E. ctenoides* S n ze (Fig. 31) is characterized by the little flexed braincase, the well-developed preorbital pits, the large ethmoidal openings with very short contact interval with nasals (about 30% of the ethmoidal opening length); the small oval bullae tympani with a longitudinal ridge; and the broad, bell-shaped, widened in pharyngeal tuberosities basioccipitale. The posterior edge of nasal bones almost reaches the line connecting the anterior edges of orbits. The dentition generally is primitive: the P_4 normally is not molarized, the lower premolar series is moderately short (premolar/molar ratio varies between 55% and 67%), the upper molars occasionally are supplemented with a small protoconal fold and a hypoconal spur, the entostylids are small. It is not clear if upper canines are present or not, since all specimens that I studied are damaged in their rostral part, so I could not verify this character.

The area of distribution of *E. ctenoides* is rather limited and includes only Western and Mediterranean Europe (Croitor & Bonifay 2001). This is a polymorphic species

represented by several local and chronological forms distinguished mainly by morphological details of antlers (Azaroli & Mazza 1992; De Vos et al. 1995). Today, many authors place the numerous species names (*senezensis*, *darestei*, *falconeri*, *tegulensis*, and *tetraceros*) in the list of synonymy of *Eucladoceros ctenoides* (De Vos et al. 1995; Croitor & Bonifay 2001; Valli & Palombo 2005; Baygusheva & Titov 2013). Perhaps, some local and chronological variants of *E. ctenoides* could be maintained as subspecies:

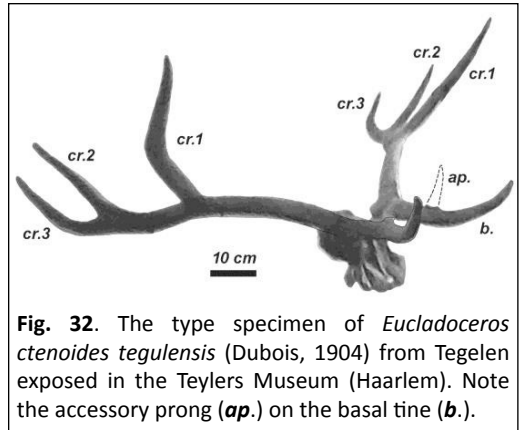


Fig. 32. The type specimen of *Eucladoceros ctenoides tegulensis* (Dubois, 1904) from Tegelen exposed in the Teylers Museum (Haarlem). Note the accessory prong (*ap.*) on the basal tine (*b.*).

E. ctenoides vireti Heintz, 1970; *E. ctenoides tetraceros* Dawkins, 1878; *E. ctenoides tegulensis* (Dubois, 1904); and *E. ctenoides falconeri* (Dawkins, 1868) (= *E. darestei* [Deperet, 1931], = *E. senezensis* [Deperet & Mayet, 1910]). *E. ctenoides ctenoides* from Upper Valdarno possess the primary type of antler morphology with respect to the more evolved antlers of *E. ctenoides falconeri* with less pronounced metamery, and the slim antlers of *E. ctenoides tetraceros*, which possibly evolved in the direction of degeneration or under the conditions of starvation. The holotype of *E. ctenoides tegulensis* (Dubois, 1904) from Tegelen exposed in the Teylers Museum (Haarlem, The Netherlands) is distinguished by peculiar flattened basal tines and an apparent presence of additional prongs (Fig. 32), which are broken off and never appeared on earlier published figures (Spaan 1992: fig. 1). Thus, I prefer to keep *E. ctenoides tegulensis* as a separate subspecies because of this unusual morphological feature. The European forms of *Eucladoceros* most probably evolved from the Asian immigrant *Eucladoceros aff. boulei* (Fig. 29, F) reported from Kapetanios, Greece (Steensma 1988).

Genus *Praemegaceros* Portis, 1920

Portis (1920: 136) proposed *Praemegaceros* as a subgenus of the genus *Cervus* with a single species *C. (Praemegaceros) dawkinsi*, Newton. Some decades later, Kahlke (1956) introduced the genus name *Orthogonoceros* with the type species *Cervus verticornis* Dawkins. Later on, Kahlke (1965) recognized the priority of Portis' (1920) *Praemegaceros*. Radulesco & Samson (1967) acted as the first reviewers of the genus: they proposed the genus definition and explicitly designated *Cervus dawkinsi* Newton as the type species. In the same publication, Radulesco & Samson (1967) proposed the new genera *Allocaenelaphus*, *Psecupsoceros*, and *Nesoleipoceros* that are synonyms of *Praemegaceros sensu* Kahlke (1965) (Croitor 2006b). The genus includes several Early and Middle Pleistocene continental giant forms with the estimated body mass ranging between 300 and 500 kg, and two lineages of medium-sized or even dwarfed forms that survived in the insular and/or refugial isolation on the Corso-Sardinian Massif and the island of Great Britain. Radulesco & Samson (1967) and Azzaroli & Mazza (1993) regarded the genus *Eucladoceros* as a forerunner for *Praemegaceros*, seeking the support for this hypothesis in the analogous general construction of antlers.

Praemegaceros is distinguished from *Eucladoceros* by larger body size and complicate shape of antlers that never show the metameric bauplan. The advanced Middle and Late Pleistocene species of *Praemegaceros* are characterized by significant anteroposterior compression of pedicles and their stronger divergence, the basal tines are reduced, sometimes represented by vestigial rudiments or completely vanished, while their distal parts are expanded into variously shaped palmations (Azzaroli 1979; Croitor 2006b). The mosaic combination of morphological details of antlers and teeth suggest that *Praemegaceros* is a paraphyletic group that includes three more or less closely related lineages. I proposed to regard these lineages as the subgenera within the genus *Praemegaceros* (Croitor 2006b). Possibly, the morphological affinity between the *Praemegaceros* lineages represent rather a morpho-funtional and eco-morphological parallelism that evolved in similar environmental conditions.

Subgenus *Praemegaceros* Portis, 1920

The antler beam is set obliquely with respect to the antler burr. The subbasal tine resting on the antler burr is present as a specific diagnostic character, however, it may be vestigial in advanced forms. The dorsal tine is in the medial position with respect to the subbasal tine (the dorsal position if the antler beam is in the natural orientation on the skull). It may be very large or vestigial. A well-expressed rib extends from the subbasal tine to the dorsal one. The antler beam is straight in the area of the dorsal tine. The subbasal tine and the middle tine are oriented in the same plane on the anterior side of antler beam. The upright curvature of the antler beam in the area of posterior tine is present only in archaic forms. Molars are devoid of the lingual cingulum and the protoconal fold.

PRAEMEGACEROS (PRAEMEGACEROS) OBSCURUS (AZZAROLI, 1953)

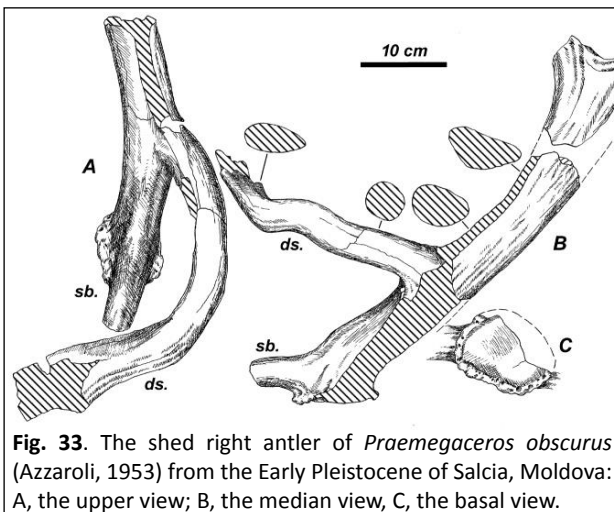


Fig. 33. The shed right antler of *Praemegaceros obscurus* (Azzaroli, 1953) from the Early Pleistocene of Salcia, Moldova: A, the upper view; B, the median view, C, the basal view.

This large cervid (ca. 400 kg) was known under several species names. Azzaroli (1953) described "*Cervus*" *obscurus* as a species with uncertain systematical position. Radulesco & Samson (1967) described from the early Pleistocene of Rotbav-Silvestru (Romania) new genus and species *Allocaenelaphus arambourgi*. Azzaroli & Mazza (1992b) described a fine antlered skull from the latest Villafranchian of Pietrafitta as

a new species *Megacerooides boldrinii*. Abbazzi (1995) restored "*Cervus*" *obscurus* Azzaroli 1953 as a valid species name and included *Megacerooides boldrinii* in the synonymy of "*C.*" *obscurus*. Croitor

(2006b) added to the synonymy of *P. obscurus* the species name *Allocaenelaphus arambourgi*.

P. obscurus is characterized by the long and strong subbasal and dorsal tines (Fig. 33). The dorsal tine may be flattened in its distal part, extremely long (more than 800 mm) and intricately curved, as it may be seen in the specimen from Cava Liberatori (Abbazzi 1995: pl. 1, fig. 1-2). The middle tine appears in fully grown antlers and is set on the anterior side of the beam. The posterior tine is developed in adult individuals. The antler beam is sharply bent in the area of posterior tine. The distal portion of antlers is not palmated.

The condylobasal length of skull from Pietrafitta (IGF 4024; MGUF) amounts to 470 mm, the length of upper tooth row amounts to 141.8 mm (P^2 - P^4 – 61.3 mm; M^1 - M^3 – 84.0 mm), the distance between P^2 and the tip of praemaxillae bones is ca. 143 mm; the nasal bones are quite long (188.4 mm), however, they do not extend behind the line connecting the anterior edges of orbits; the distance between orbits and the tip of praemaxillae bones amounts to 270 mm (the facial part is longer than in *Eucladoceros*); pedicles are short, robust, moderately diverged, and slightly compressed mediolaterally (DAP×DLM = 53.6 mm × 42.5 mm, *dx*); upper canines are missing; P_4 is molarized. The frontal bones before pedicles are slightly concave. A weak bony rib borders each pedicle base from its internal side. The parietal bones are flat. The relative length of face is similar to deer of the same size group like *Cervus*, *Megaloceros* or *Eucladoceros*. The praeorbital fossae are large and deep. The ethmoidal openings are large. The praemaxillary bones are characterized by a rather broad anterior part (Abbazzi 1995). The naso-praemaxillary suture is long and amounts to 12.5% of the total length of praemaxillary bone. The basioccipitale is bell-shaped and broadened the area of pharyngeal tuberosities (Croitor 2006b). The mandibular pachyostosis is not developed. The lingual wall of P^2 is cleft (the protocone and hypocone are fully separated each from another). The protocone and hypocone are partially separated in P^3 so its lingual wall is divided by a vertical groove. The hypocone of P^2 and P^3 is supplemented with the interior enamel fold. The lower premolar series is relatively short for such an archaic deer (the premolar / molar ratio amounts to 60%). Lower fourth premolar (P_4) is molarized.

The remains of *P. obscurus* are common in the late Villafranchian deposits of Central Italy, Central Romania, Moldova, and the Forest-bed Formation of England. Some sparse remains of *P. obscurus* are found in the late Villafranchian of Ceyssaguet (France) in the Tamaian fauna of Semibalki-1 (Azov Region, Russia), the Early Pleistocene of Ubeidiya (Israel) and Dmanisi (Georgia) (Croitor & Bonifay 2001; Croitor 2006b; Vekua & al. 2010). *P. obscurus* is the only species of the genus that was recorded in the Near East.

The oldest remains of this species come from Dmanisi dated back to 1.81 Ma (Vekua et al. 2010), suggesting the South Asian origin of the species. The answer on origin of *P. obscurus* should be sought in the paleontological record of Sivalik Hills. Azzaroli (1954) reported from the Sivaliks a rather large cervid similar to *Eucladoceros* (*Euctenoceros* [?] *sp.* fide Azzaroli 1954: fig. 7a) that is represented by a proximal fragment of a shed

antler characterized by the strong basal tine and two accessory prongs just above the basal ramification. Here should be mentioned also the antlers of "*Rucervus sp. l*" from the Sivaliks (BM41834b, BM41834c, 41834d in Azzaroli 1954: fig. 6) characterized by the comparatively low position of the first tine, the very obtuse angle of the first ramification, the strong backward bending of the beam at the level of the first ramification, the occasional presence of accessory prongs above the first ramification, and the small distal bifurcation (Azzaroli 1954). As Azzaroli (1954) reasonably noticed, the enlisted characters correspond to the modern *Panolia eldi*. In my opinion, the attribution of "*Euctenoceros sp.*" antler from the Sivaliks to *Panolia sp.* is plausible. Most of the enlisted antler characters of *Panolia sp.* from the Siwalik Hills (the strong basal tine, the strong backward bending of the beam, and the obtuse angle of the first ramification) correspond to the antler morphology of *P. obscurus*. The accessory prongs in the area of the first ramification are also common for modern *Panolia eldi* and recall the position of the dorsal tine in *P. obscurus*. Therefore, one can assume that *P. obscurus* is a large-sized descent of *Panolia sp.* from the Sivaliks.

PRAEMEGACEROS (PRAEMEGACEROS) DAWKINSI (NEWTON 1882)

The species was described from the middle Pleistocene of Cromer Forest-bed Formation. Dawkins (1872), who studied the remains of this species for the first time, regarded it as a juvenile individual of *Praemegaceros verticornis*. Newton (1882) described the "juvenile" antler as a new species *Cervus dawkinsi* and designated the specimen figured by Dawkins (1872: fig. 1) as a holotype. Portis (1920) included *C. dawkinsi* in the subgenus *Cervus (Praemegaceros)*. Finally, Kahlke (1956) designated *C. dawkinsi* as the type species of the genus *Praemegaceros*. Since *Cervus belgrandi* from France is a synonym of *P. verticornis* (see below the remarks on taxonomy of *Praemegaceros verticornis*), the presence of *P. dawkinsi* on the Continental Europe is not confirmed.

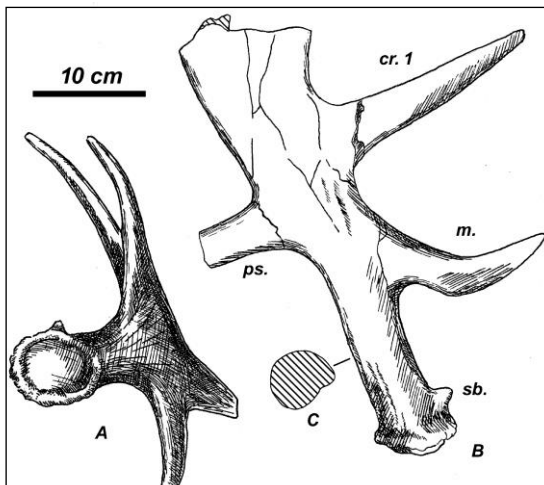


Fig. 34. The left shed antler M18706 (NHML) of *Praemegaceros dawkinsi* (Newton, 1882) from Mundesley, Norfolk: A, the basal view; B, the median view; C, the beam cross-section.

P. dawkinsi is a medium-sized deer with mesodont dentition and short antlers terminated with palmations. The body mass estimation based on mandibles ascribed by Azzaroli (1953) to this species amount ca. 220 kg. The subbasal tine normally is vestigial; in some cases, it may be absent (as in the antler M18168, NHML) or more or less well-developed as in *P. obscurus* (the type specimen) or present as a vestigial knob. The dorsal tine may be missing as well (as in the specimen M18706, Fig. 34) or may be present as a vestigial knob (Croitor 2006b). The middle and the posterior tines are developed. The sample of eight available specimens shows the

subbasal tine maintained as a small button only in three specimens of *P. dawkinsi*. Five specimens lack the subbasal tine rudiment. The rudiment of dorsal tine is present in three specimens only. Four antlers (50% of the sample stored in NHML) lack any vestiges of proximal tines. The antler beam is set obliquely with respect to the burr plane as in *P. obscurus*. A groove-like depression bordered by a rib extends from the basal rudimental tine to the middle tine is seen in the antler M18706 recalling the morphology of *P. obscurus*. However, unlike *P. obscurus*, the beam is straight, without curves in the areas of dorsal and posterior tines. The antler portion above the posterior tine is shortened. The antler extends into a small palmation beginning from the first crown tine.

The mandibles M17675 (old number 339) and M6224 (NHML) ascribed by Azzaroli (1953) to *P. dawkinsi* are characterized by primitive P_4 and comparatively long premolar series: the premolar/molar series length ratio amounts to 63.3% and 68.2% respectively. Azzaroli (1953) reports a pachyostosis of lower mandible in *P. dawkinsi*, however the mandibles seems to have the normal shape (the mandible thickness below M_2/M_3 is 26.5 – 24.4 mm).

The pedicles are very divergent, short, robust and compressed dorsoventrally as in the giant species with heavy antlers *P. verticornis* and *P. solilhacus*. The sideward orientation of palmated antlers and the shape of pedicles suggest that the evolution of *P. dawkinsi* passed through the stage of a giant form with large heavy antlers.

PRAEMEGACEROS (PRAEMEGACEROS) MOSBACHENSIS (SOERGEL, 1927)

The deer from the lower level of Mosbach is characterised by a very large size, strongly divergent antlers and a well-developed subbasal tine (Soergel 1927). The dorsal tine in the type specimen is present on the right antler only. The antlers extend into a broad flattening above the middle tine. The deer from Mosbach is very close to *P. obscurus*, but is more advanced in shape of its antlers. Azzaroli (1953) included *P. mosbachensis* in his informal “*verticornis*” group. Kahlke (1956) and Vislobokova (2013) included *P. mosbachensis* in the synonymy of *P. verticornis*, accepting an extremely vast individual variation of antler morphology for this deer. In my opinion, *P. mosbachensis* and *P. verticornis* represent a good example of parallelism, since most probably they evolved similar eco-morphological adaptations independently. Some details of antler morphology suggest that those two cervid forms belong to different phyletic lineages: *P. mosbachensis* maintains the well-seveloped subbasal tine, while the lineage of *P. vertivornis* lost this feature during the evolutionary transition between *P. pliotarandoides* and *P. vesticornis*. The antler beam in *P. mosbachensis* becomes flattened in the area of middle tine, while *P. verticornis* always is characterised by the cylinder-shaped beam even in forms, which evolved distal palmations, as, for instance, in the antlered skull from Pakefield (Harmer 1899). Radulesco & Samson (1967) has pointed already out that the antlers of the deer from Mosbach recall *P. dawkinsi*. Apparently, *P. mosbachensis* represents a transitional evolutionary link between *P. obscurus* and *P. dawkinsi*, therefore its specific status should be maintained.

Subgenus *Nesoleipoceros* Radulesco & Samson, 1967

This subgenus includes several dwarfed insular forms from Corsica and Sardinia and a giant mainland form. The proximal portion of antler beam is cylindrical; the distal portion of antler is compressed lateromedially and normally is extended into a palmation. Unlike the subgenera *Orthogonoceros* and *Praemegaceros*, the antlers of *Nesoleipoceros* have not a dorsal tine situated on the upper side of the beam; the beam does not form a sharp curvature in the area of the posterior tine. The subbasal tine is present as a vestigial knob or completely disappears. The basal tine is sometimes present and is inserted on the anterior side of the beam. The middle tine is well-developed, compressed dorsoventrally and may form a small terminal palmation. The posterior tine is present in fully-grown antlers. The crown tines are inserted on the anterior and posterior side of the beam; the posterior tines form a palmation of variable size and shape. The lower fourth premolar normally is not molarized and generally is more primitive if compared to the deer of the subgenera *Orthogonoceros* and *Praemegaceros*.

PRAEMEGACEROS (NESOLEIPOCEROS) CAZIOTI (DEPÉRET, 1897)

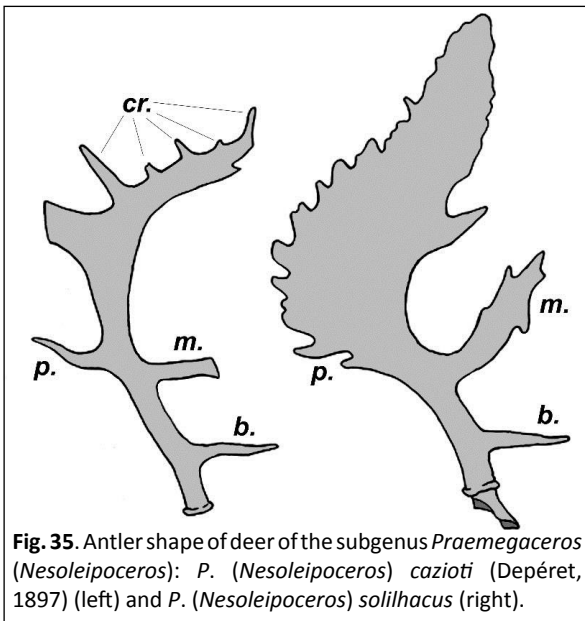


Fig. 35. Antler shape of deer of the subgenus *Praemegaceros* (*Nesoleipoceros*): *P. (Nesoleipoceros) cazioti* (Depéret, 1897) (left) and *P. (Nesoleipoceros) solilhacus* (right).

This species is slightly larger than modern fallow deer. Its antler beam is compressed dorsoventrally in its proximal part. The distal part of antler is compressed lateromedially. The subbasal and dorsal tines are missing. The basal tine is straight, sharp, situated on the lateral side of the beam and pointed toward the anterior (Depéret, 1897). The middle tine is compressed dorsoventrally. The position of posterior tine may be variable with respect to the middle tine. A small palmation of variable size is developed on the posterior side of the third quarter of beam (Fig. 35). Several prongs and digitations may occur on the

palmation's edge. The most distal part of antler is also flat, but is not palmated. The terminal part of antler has several small crown tines on its anterior and posterior sides. The burr is set obliquely with respect to the beam.

The cranial morphology is not "paedomorphic" and maintains the normal proportions for a deer of such body size (Croitor et al. 2006). The frontal bones are flat with a depressed sagittal profile between orbits. The supraorbital openings are very large. The pedicles are short, slightly compressed anteroposteriorly, moderately divergent and

sloped caudally (Fig. 36). The face length amounts approximately to $\frac{1}{2}$ of the total skull length as in mainland deer of the similar size (*Dama dama*, *Axis axis*) and is just slightly shorter than the face length in *P. obscurus* and *E. senezensis*. The anterior edge of orbit is situated above M^3 that may be correlated with the relatively large tooth row length. The basioccipitale is bell-shaped with the broadened area of pharyngeal tuberosities (Fig. 36, C). The nasal bones do not reach behind the line connecting the anterior edges of orbits. The ethmoidal openings normally are developed, however, they may be reduced in some cases. The praemaxillary bones are broad and square-shaped. The mandibular pachyostosis is not developed (Croitor et al. 2006). The general shape of skull is similar to *Eucladoceros*, but the face morphology and the masticatory apparatus show some peculiar characters resulted from the extreme adaptation to grazing, which is particularly advanced in *P. cazioti* from the late Würm site of Dragonara, Sardinia (Caloi & Malatesta 1974). Unlike *Eucladoceros*, the protoconal fold is never present in upper molars. The lingual wall of P^2 is not cleft, nor segmented by a vertical groove, thus the protocone and hypocone are not separated. The lingual wall of P^3 is not grooved. The hypocone in both P^2 and P^3 is supplemented with an internal enamel fold. The upper molars have a small entostyle and a hypoconal enamel fold, which may be absent. P_4 is never molarised. Metapodials are very thin.

Two chronosubspecies are recognized (Croitor et al. 2006). *P. cazioti algarensis* Comaschi Caria, 1956 from the late Würm sites of Algero and Dragonara (Sardinia) is a more specialised grazing form characterised by the larger body size. Its upper cheek teeth are large (the upper tooth row attains one third of the condylobasal skull length) and mesodontous. The premolar series is relatively long: the premolar/molar length ratio varies between 62.7% and 64.5%. The diastema of the lower mandible is shorter than $\frac{1}{2}$ of the lower tooth row length. The area of musculus masseter insertion on the lower mandible is larger and extends toward the anterior until M_3 level. The preorbital fossae are reduced.

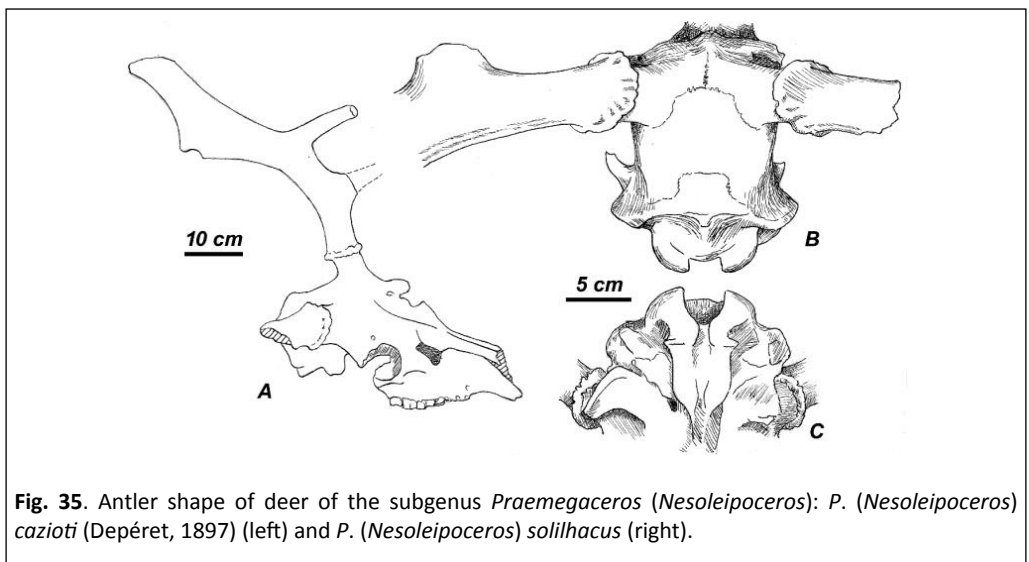


Fig. 35. Antler shape of deer of the subgenus *Praemegaceros* (*Nesoleipoceros*): *P. (Nesoleipoceros) cazioti* (Depéret, 1897) (left) and *P. (Nesoleipoceros) solilhacus* (right).

P. cazioti cazioti (Depéret, 1897) from the Riss-Würm sites Maccinaggio and Coscia (Corsica) is smaller and is characterised by the relatively smaller and brachydontous teeth. The relative length of upper tooth row is below 30 % of the condylobasal skull length. The diastema is longer than 1/2 of the lower tooth row length. The series of lower premolars is relatively short; the ratio between lower premolar and molar series often is below 60 %. The area of m. masseter insertion on the lower mandible is reduced and does not reach the level of M₃. The preorbital fossae are normally developed.

Van der Made & Palombo (2005) described a somewhat larger species *Praemegaceros sardus* from the Middle Pleistocene (ca. 450 ka) of Sta. Lucia 1 (Sardinia). The metapodials of *P. sardus* are more robust, while its linear measurements are 25-40 % larger than those of *P. cazioti*. Another endemic form of *Praemegaceros (Nesoleipoceros) sp.*, still larger and older (>450 ka), was reported from the Su Fossu de Cannas Cave, Sardinia (Melis et al. 2016). *Cervus elaphus rossii* Pereira, 2001 from the Middle Pleistocene of Castiglione Cave (Corsica), apparently, is very close or even identical to *P. sardus* or to the unnamed yet deer from Su Fossu. The morphology of upper and lower teeth figured by Pereira (2001) is very similar to that of *P. sardus*, but just slightly larger. The limb bones of the deer from Castiglione are relatively robust (Pereira 2001). Despite of the restricted number of remains, there is no doubt that the Castiglione cervid *Praemegaceros (Nesoleipoceros) rossii* (Pereira, 2001) belongs to the *P. sardus* – *P. cazioti* lineage.

PRAEMEGACEROS (NESOLEIPOCEROS) SOLILHACUS (ROBERT, 1830)

This is the largest (420 kg) species of *Praemegaceros* with unclear phylogenetic relationships with other continental species of the genus. *Praemegaceros solilhacus* was described by Robert (1830) from the early Middle Pleistocene of Soleilhac (Central Massif, France). The neotype 2003-4-346-SOL (MCP) is a partially destroyed left frontal bone with a proximal part of antler lacking the distal part right above the posterior tine (Azzaroli 1979). The pedicle is compressed in the dorsoventral direction as in *P. verticornis* and *P. dawkinsi*. The maximum diameter of the pedicle is 79.0 mm; the maximum diameter of the burr is 101.0 mm. The antler beam is set obliquely on the burr and is directed more or less sideward. The antler base is of oval shape, compressed in the dorsoventral direction. The type antler is devoid of basal tines or their vestiges. The antler beam becomes significantly flat in the area of the middle tine situated at 215 mm from the burr and slightly bends toward the posterior. In the area of the posterior tine, the beam curves gently toward the anterior. A groove-like longitudinal depression ranges on the anterior side of the antler beam from the middle tine to the burr.

The bauplan of the complete left antler 2003-4-397-SOL (MCP) of *P. solilhacus* strikingly reminds the antler construction of *P. cazioti* (Fig. 35) that allowed us to assume the close phylogenetic relationship between those two species (Croitor et al. 2006). The straight length of the antler 2003-4-397-SOL amounts to 1300 mm; the diameter of its pedicle amounts to 79.0 mm; the diameter of antler base amounts to 84.0 mm. The proximal part of the antler bears a long straight basal tine, which is missing in the lectotype. It seems that the development of the basal tine is a variable character in this

species. It is preserved as a vestigial knob in the shed antler from the Tiraspolian gravel (Croitor et al. 2006).

The distal palmed portion is gently curved and elevated, but does not form a sharp curvature as in *P. verticornis* and *P. pliotarandoides*. The antler extends into a large palmation just above the posterior tine. The palmation has a leaf-like shape with small digitations on its posterior edge. The anterior part of palmation has a single sharpened prong. The middle tine is terminated with a small palmation with digitations. Unlike *P. verticornis* and *P. obscurus*, the dorsal tine in *P. solilhacus* never occurs. The antler bauplan of *P. solilhacus* also is very different: the distal palmation seems to be derived from posterior crown ramifications (Vislobokova 2012). This type of antler construction is known also in *Rucervus*, however, unlike *Rucervus*, *P. solilhacus* and *P. cazioti* possess a well-developed middle tine.

We know very little about the cranial morphology of *P. solilhacus*: its frontal bones are flat and just slightly depressed before pedicles.

The length of tooth row of the mandible 2003-4-439-SOL (*sin*, MCP) (Azzaroli 1979: pl. 3, fig. 3-3a) is 156.3 mm. The premolar/molar series length ratio amounts to 62% (Table 3). The mandibular body is comparatively high. The diastema is moderately long: it is slightly longer than lower molar series and attains 65.6% of the lower dentition length. The mandibular pachyostosis is not developed. P_4 is variable in morphology, but often is not fully molarized. The lower molars are supplemented with ectostylids.

The upper cheek tooth row 2003-4-421-SOL (*sin*, MCP) possibly corresponds to the upper maxilla figured by Robert (1830: pl. II, fig. 4). The upper molars and premolars have the weak cingulum-like basal structures. The lingual side of P^2 is divided by the vertical groove. This character distinguishes *P. solilhacus* from *P. cazioti*. The hypocone of premolars is supplemented with additional interior enamel fold. The upper molars are characterised by an enamel fold in posterior wing of hypocone. The M^1 and M^2 have an additional enamel fold on the anterior wing of hypocone. The enamel of posterior wing of protocone is undulated.

The remains of *P. solilhacus* were reported from the early Middle Pleistocene faunas of France, Germany, Italy, South Russia and Moldova (Azzaroli & Mazza 1993; Croitor et al. 2006). Apparently, *P. solilhacus* became extinct by the end of the Mindel glaciation.

Subgenus *Orthogonoceros* Kahlke, 1956

Deer of this group are characterized by strongly divergent (almost horizontal in their proximal part) cylinder-shaped antler beam, a well-developed cylinder-shaped dorsal tine situated on the median side of the beam (the upper side if the antler is seen in its natural position on the skull) and curved toward the anterior, a vertical position of the antler base with respect to the burr plane, a sharp curve of the antler beam in the area of posterior tine that cause the vertical orientation of the distal crown part of antlers. The subbasal tine may be represented by a small vestige or completely missing. The basal tine is missing. The cylindrical dorsal tine is inserted on the upper side of the

beam and bends toward the anterior. The posterior tine is normally present in the fully-grown antlers. The crown tines are oriented in the parasagittal plane. P_4 normally is molarized.

PRAEMEGACEROS (ORTHOGONOCEROS) PLIOTARANDOIDES (DE ALESSANDRI, 1903)

This large-sized species (400 kg) with comparatively simple antlers was described from the Early Pleistocene (Galerian) of Cortiglione Monferrato, North Italy (De Alessandri 1903: 11, fig. 4-5). *Psekupsoceros orientalis* Radulesco & Samson, 1967 is a junior synonym of *P. pliotarandoides* (Croitor & Kostopoulos 2004). *P. pliotarandoides* is characterized by the presence of a cylinder-shaped curved dorsal tine and a hook-like posterior tine. The middle tine is never developed. The specimen from the type locality lacks its distal portion, however, the fine complete antlers discovered mostly in Eastern and Southeastern Europe show a constant shape of the crown part: the beam above the posterior tine is dichotomously branched and then each branch in its turn is terminated with a dichotomous bifurcation (Fig. 37). The antler crown is oriented in the parasagittal plane; a small subbasal tine above the burr is normally present, but may be reduced to a knob-like vestige (Melentis 1967; Radulesco & Samson 1967; Baygusheva 1994; Croitor & Kostopoulos 2004). According to Radulesco & Samson (1967), the vestigial subbasal tine is not present in the majority (76.29%) of *P. verticornis* specimens from Süßenborn; only a knob-like rudiment is observable in 21.65 % of specimens, while a clearly expressed basal tine is recorded in 2.06 % of specimens. Apparently, the vestigial subbasal tine in *P. pliotarandoides* is analogous to the long and massive subbasal tine in *P. obscurus*, thus suggesting a close relationship between those two species.

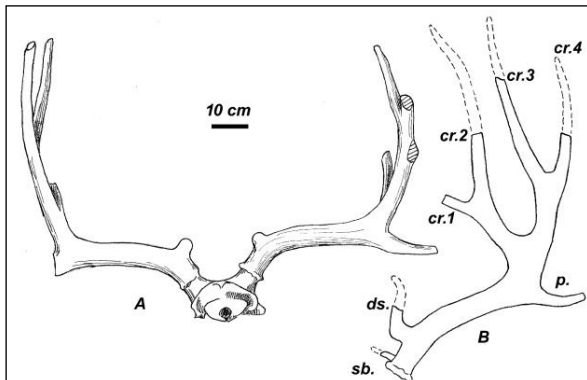


Fig. 37. The antlered braincase of *Praemegaceros (Orthogonoceros) pliotarandoides* (De Alessandri, 1903) from the late Early Pleistocene of Haliakmon, Greece: A, the posterior view; B, the median view of right antler (Adapted from Melentis 1967).

Kahlke (1956) and Azzaroli (1976, 1979) believe that *Cervus pliotarandoides* De Alessandri represents an individual variation of *P. verticornis* and included it in the synonymy of the latter species. However, *P. pliotarandoides* differs from *P. verticornis* in the absence of medial tine and the frequent presence of basal rudimentary tine (spurious tine) right above the burr. This, obviously, less evolved variant of *verticornis*-type antlers is found only in older Early Pleistocene faunas characterized by the absence of red deer *Cervus*

elaphus. The Russian authors traditionally regard De Alessandri's deer as *Eucladoceros pliotarandoides*, apparently, because of the dichotomously branched crown tines that remind the dichotomously branched crown tines of *E. dicranios* (Verestchagin

1959; Flerov 1962; Alekseeva 1977; Vislobokova 1990; Baygusheva & Titov 2013). However, *P. pliotarandoides* does not show the comb-like bauplan of antlers that is the important diagnostic characters of *Eucladoceros*, while the dichotomous bifurcation of crown tines appeared in the antler evolution of cervids independently several times (for instance, *Rucervus schomburgki*, *Blastoceros dichotomus*).

Complete skulls are not known. The frontal bones are depressed in the front of pedicles, with the slightly concaved or straight sagittal profile. The angle of divergence between pedicles is about 90°. The pedicles are robust, with circular transversal cross-section and may be just slightly compressed anteroposteriorly. The *basiossipitale* is bell-shaped and broadened in the area of pharyngeal tuberosities. *Foramen ovale* is very large.

As one can see in the upper dental row APL-243 from Apollonia (Croitor & Kostopoulos 2004: fig. 4, B) and in the upper dentition figured by Flerov (1962), the lingual wall of P² is not cleft, the interior wall of premolar hypocone is slightly folded, unlike those in *Eucladoceros* and *P. obscurus*. The upper molars have no protoconal fold which characterize *Eucladoceros*, neither the spur of hypocone that may be found in both *Eucladoceros* and *P. obscurus*. The advanced stage of P₄ molarization in *P. pliotarandoides* from Apollonia (APL-491, *sin*; APL-402, *dex*) also distinguishes this deer from *Eucladoceros*. The lower premolar series of the single known complete mandible from Apollonia is comparatively long: the premolar/molar ratio amounts to 70.7% and 72.8%. The mandible is not pachyostotic.

P. pliotarandoides appears to be a characteristic element of pre-Galerian and Galerian faunas of South and South-East Europe. Remains of *P. pliotarandoides* are found in Italy, North Greece, Moldova, South Ukraine and Azov Sea Region (Croitor & Kostopoulos 2004). *P. cf. obscurus* from Barranco Leon-5 (Martinez-Navarro et al. 2004) lacks the characteristic of *P. obscurus* subbasal tine and is rather close to *P. orientalis*, but the distal portion of the antler under discussion is simplified, which may be just an individual morphological variant or represent a taxonomically meaningful character (Fig. 38). One cannot exclude that *Praemegaceros* from Barranco Leon-5 is an endemic Iberian species closely related to *P. orientalis*.

PRAEMEGACEROS (ORTHOGONOCEROS) VERTICORNIS (DAWKINS, 1872)

Dawkins (1872: 407) based his description of *Cervus verticornis* on the proximal fragment of a robust shed antler, which supposedly comes from the beach near Pakefield, Norfolk from the Cromer Forest-Bed Formation. Harmer (1899) described the well-preserved antlered skull from Pakefield (M11352, NHML) as *Cervus belgrandi* Lartet, which was regarded as a senior synonym of *Cervus verticornis*. Azzaroli (1953)

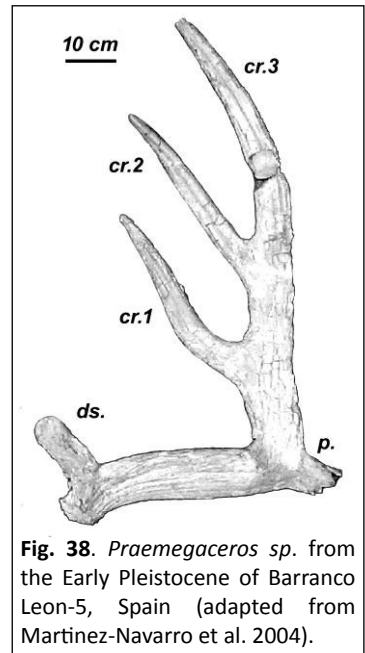


Fig. 38. *Praemegaceros* sp. from the Early Pleistocene of Barranco Leon-5, Spain (adapted from Martinez-Navarro et al. 2004).

and Radulesco & Samson (1967) supposed that "*C.*" *belgrandi* is close to *P. dawkinsi* and possibly identical with it. This viewpoint was followed by Croitor (2006b). The species name *Cervus belgrandi* appears for the first time in the poorly known publication of Belgrand (1883: pl. 7, figs. 1-2; pl. 8, fig. 1). According to Belgrand (1883), this is a large-sized deer (the frontal breadth is 170 mm) approaching the dimensions of *Megaceros*. This cervid form is characterized by the strongly divergent antlers and the typical for *P. verticornis* dorsal tine. The antler figured by Belgrand (1883) on fig. 1 of pl. 8 has a vestigial dorsal tine as in *P. dawkinsi*, however, its size is large and the beam in the area of the middle tine is not flattened. Therefore, *Cervus belgrandi* Belgrand, 1883 should be regarded as a *nomen oblitum* synonymous with *Praemegaceros verticornis*.

The cast of lectotype M40835 (NHML) represents a basal fragment of left shed antler that belongs to a large mature individual (Croitor 2006b: fig. 18). The antler base is circular, compressed in the anteroposterior direction. The maximal diameter of the antler base amounts to 92.0 mm; the circumference of antler base amounts to 275.0 mm. The subbasal tine is not developed. The dorsal tine is situated on the dorsal side of the beam. The distance between the tine base and the antler burr amounts to 42 mm. The preserved part of the dorsal tine is cylindrical and is curved toward the anterior and downward. An accessory button-like prong is situated on the lateral side of the antler beam close to the dorsal tine and apparently represents a sort of hypermorphism. The presence of the middle tine that springs off on the anterior side of the beam is a diagnostic character distinguishing *P. verticornis* from *P. pliotarandoides*. The antler beam is somewhat compressed dorsoventrally between the dorsal and middle tines.

The constant character of the middle tine development in *P. verticornis* is an important question for the diagnostic differentiation of *P. verticornis* from *P. pliotarandoides*. According to H.-D. Kahlke (personal communication to Croitor & Kostopoulos 2004), the middle tine is always present in *P. verticornis* from younger deposits of Mosbach and Süßenborn. The middle tine is also always present in the British specimens of *P. verticornis* described by Dawkins (1872, 1887) and therefore it cannot be considered as a variable feature. Pfeiffer (2002) described a skeleton of the two-year old antlered *P. verticornis* stag from Bilshausen (Germany) that already possess the strong and very long middle tine, as well as the dorsal, posterior and crown tines. The finding from Bilshausen proves that the middle tine is present in *P. verticornis* at a very early stage of the ontogenetic development. The pedicels of *P. verticornis* are strongly sloped backward and sideward and strongly compressed in the dorsoventral direction.

The shape of distal portion of antler may vary. The most complete antlers from Süßenborn have slightly compressed from the sides branched tines (Kahlke 1956), which, apparently, are analogous to the crown shape of *P. pliotarandoides*. The antlered braincase from Pakefield (England) is different. Its distal part is extended into a broad fan-shaped palmation (Harmer 1899). The antlers of *P. verticornis* with simple branched and palmated distal parts apparently may have a taxonomic significance at the subspecies or even species level. Unfortunately, this question have no solution, since the type specimen of *P. verticornis* lacks its distal part.

The complete skulls of *P. verticornis* are not known. The braincase is relatively short and broad. The basioccipitale is broad and bell-shaped. The frontal bones are flat, with compressed dorso-ventrally pedicles. The pedicles are sloped sideward and backward and are oriented in the forehead plane. The shape and position of pedicles is a taxonomic character distinguishing *P. verticornis* from *P. politarandoides*. P_4 usually is molarized. The lingual walls of upper premolars are not cleft or grooved. The hypocone of premolars is supplemented with a small interior enamel fold. The pachyostosis of lower mandible is not developed (Croitor 2006b).

Genus *Praedama* Portis 1920

Portis (1920) included in his subgenus *Cervus* (*Praedama*) an eclectic group of species from the Late Pliocene and Pleistocene of north-western Europe: *C. (Praedama) falconeri* Dawkins (now is in *Eucladoceros*); *C. (Praedama) savini* Dawkins (= *Dolchodoryceros suessenbornensis* Kahlke, 1956; designated as type species of *Praedama* by Radulesco & Samson 1967); and *C. (Praedama) verticornis* Dawkins (now in *Praemegaceros*). This is a poorly understood genus from the final stage of Early Pleistocene and the Middle Pleistocene of Europe. This genus is often regarded as a direct forerunner of the giant deer *Megaloceros* (Azzaroli 1953; Vislobokova 1990; van der Made & Tong 2008) or its sister form (Lister 1994) and sometimes is synonymized with it (Lister 1987, 1994; van der Made 2013).

PRAEDAMA SAVINI (DAWKINS, 1887)

Praedama savini (ca. 220 kg) is known from the Middle Pleistocene of Europe (0.8-0.4 Ma). The available data on this cervid are incomplete, despite of the fine antlered frontlet found in Süßenborn, Germany (Kahlke 1969). The antler is characterized by the flattened proximal part of basal tine (the complete basal tine is not known) situated at a small distance from the burr, the middle tine, the posterior tine and the three long crown tines, two of which compose a terminal bifurcation of the antler (Fig. 39). The antler beam and the tines are compressed from the sides.

The frontlet M6301 (NHML) most probably belongs to *P. savini*. The cross-section of its pedicles below the antler burrs is circular (DLM×DAP sin = 63.1 64.8 mm; DLM×DAP dx = 65.6 64.0 mm); the pedicles are quite robust (L sin = 24.5 mm; L dx = 23.0 mm) and moderately diverged. The peculiar quadrangular cross-section of the antler base that mirrors the flattened basal tine is the most interesting morphological peculiarity of this specimen. Reliable findings of mandibles and dentition of this species are not known.

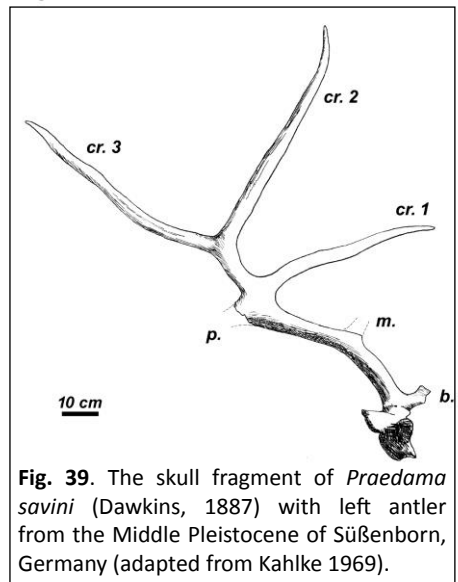


Fig. 39. The skull fragment of *Praedama savini* (Dawkins, 1887) with left antler from the Middle Pleistocene of Süßenborn, Germany (adapted from Kahlke 1969).

Van der Made (2013) described the new species *Praedama novocarthaginiensis* (= *Megaloceros novocarthaginiensis* van der Made, 2013) from the latest Early Pleistocene of Cueva Victoria (Spain) distinguished from *P. savini* essentially by its larger size. The sample from Cueva Victoria contains dental remains characterized by the simple unmolarized P₄, the folded inner wall of hypocone in the upper premolars, and the upper molars devoid of the protoconal fold and the lingual cingulum (van der Made 2013).

Azzaroli (1953) regarded the flattened basal tine of antler as an argument for the phyletic relationship between *P. savini* and *M. giganteus*. This assumption was uncritically accepted (Lister 1994; Vislobokova 1990, 2012; van der Made & Tong 2008). However, the hypothesized phylogenetic relationship between the two genera based on a single antler character is not safe. The quadrangular shape of antler base in *Praedama savini* is different from the morphological condition seen in *M. giganteus*, therefore some more strong evidences are needed to reveal the phylogenetic relationships of *Praedama*. I would like to point out the affinity between antler shape of *Praedama* and *Eucladoceros*. The specific quadrangular cross-section of the antler base in *P. savini* reminds sub-triangular cross-section of *E. dicranios* with flattened basal tine, while the whole compressed from the sides antler with three crown tines and flattened basal tine reminds the antler shape of *E. ctenoides tegulensis* (Dubois, 1904).

Genus *Cervus* Linnaeus 1758

Cervus is the most successful modern cervid genus with an extremely vast Palearctic and Nearctic distribution. Nonetheless, *Cervus* maintains the most primitive cranial morphology among all modern cervid genera from the temperate climate latitudes. The genus *Cervus* is characterized by the comparatively little flexed braincase (less than in *Dama*), the relatively longer pedicles (L=D), which are somewhat divergent and inclined caudally, the narrow triangular basioccipitale (as in *Muntiacus*), the small upper canines, and the long naso-premaxillar articulation (Heptner & Zalkin 1947; Flerov 1952). The cranial and dental advanced specialized characters are few. The facial part of skull is long mostly due to the lengthening of the orbitofrontal portion, therefore the projection of the anterior edge of orbit is situated behind the posterior edge of M³ (with the exception of *C. nippon*). The nasal bones are relatively long (longer than upper tooth row), however they do not reach the line connecting the anterior edges of orbits due to the elongated orbitofrontal portion of the skull. *Strongyloceros* Owen, 1846, *Pseudodama* Azzaroli, 1992, and *Euraxis* Di Stefano & Petronio, 1998 are junior synonyms of *Cervus*.

CERVUS NESTII (AZZAROLI, 1947)

C. nestii from the Late Villafranchian of Upper Valdarno (Italy) is the earliest representative of the genus *Cervus* in Europe. This rather small-sized (ca. 70 kg) cervid with four-pointed antlers was described by Azzaroli (1947) as *Dama nestii nestii*. Later, Azzaroli (1992) created a new genus *Pseudodama* with the type species *Dama nestii nestii* Azzaroli, 1947 and several other Late Pliocene and Early Pleistocene "*Dama-*

like” deer: *Cervus pardinensis* Croizet & Jobert, 1828; *Cervus rhenanus* Dubois, 1905; *Cervus perolensis* Azzaroli, 1952; *Pseudodama lyra* Azzaroli, 1992; and *Pseudodama farnetensis* Azzaroli, 1992. The enlisted species share the similar body size comparable to that of modern fallow deer (hence the term “*Dama*-like deer”) and the simple lyre-shaped antlers with three or four tines. The genus *Pseudodama* caused controversial opinions, however many authors agreed that *Pseudodama* is a polyphyletic taxon (de Vos et al. 1995; Croitor 2001, 2006a, 2012; di Stefano & Petronio 2002). Di Stefano & Petronio (2002) included the “*Dama*-like” species in the modern genera *Axis* (including *Cervus nestii*) and *Rusa*. Pfeiffer (1999) regarded Azzaroli’s *Pseudodama* as a subgenus of the genus *Dama*. Cranial and dental morphology involved in the study proves that some of species included in *Pseudodama* represent primitive members of modern genera *Cervus* and *Dama* (*Cervus nestii* and *Dama eurygonos*), other forms belong to the extinct lineages *Metacervocerus* and *Praeclaphus* (*Metacervocerus pardinensis*, *Metacervocerus rhenanus*, and *Praeclaphus lyra*) (Croitor 2001, 2006a, 2012).

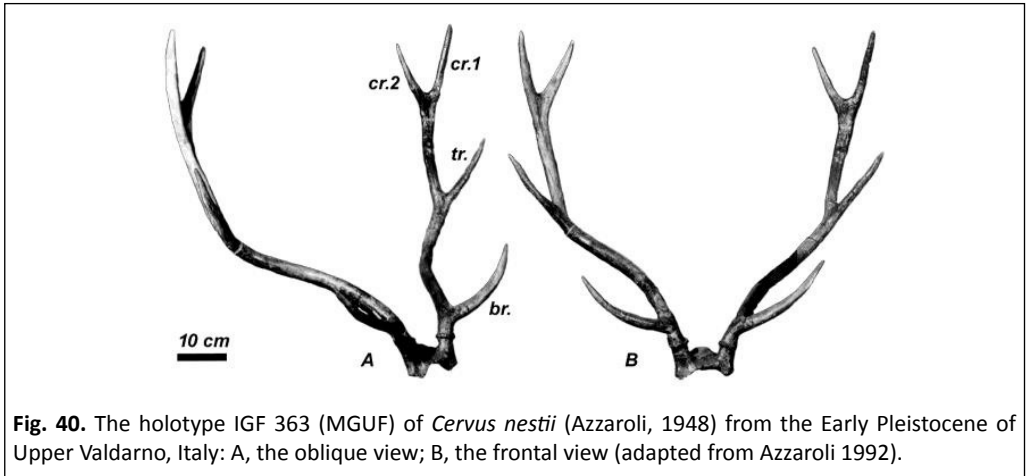


Fig. 40. The holotype IGF 363 (MGUF) of *Cervus nestii* (Azzaroli, 1948) from the Early Pleistocene of Upper Valdarno, Italy: A, the oblique view; B, the frontal view (adapted from Azzaroli 1992).

The type specimen IGF 363 (MGUF) from Upper Valdarno is a pair of antlers that belongs to a mature individual (Fig. 40). The antlers are thin, long and four-pointed. The first tine is situated at a certain distance from the burr. The bez tine (additional basal tine, which is often present in red deer) is always missing. The middle (trez) tine is well-developed. The first segment of the beam (the portion between first and middle tines) is somewhat longer than the second segment (the beam portion between the middle tine and the distal bifurcation). The distal bifurcation is formed by two short tines of almost equal size and is oriented in the frontal plane. The pedicels are moderately long (L, 19.8 mm; DAP×DLM, 27.5×30.5 mm [sin]; L, 22.5 mm; DAP×DLM, 27.1×29.5 mm [dx]) and somewhat inclined caudally. The frontal orientation of the distal fork reminds the primitive fossil and modern subspecies *C. elaphus acoronatus* and *C. elaphus bactrianus*. The antlers of *C. nestii* are very similar to those of the subspecies *C. elaphus barbarus* Bennett from North Africa that also lack the bez tine.

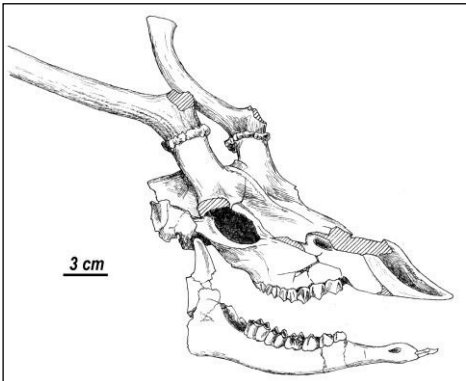


Fig. 41. The skull IGF 243 (MGUF) of *Cervus nestii* from the Early Pleistocene of Figline, Italy (oblique view).

The fairly complete but damaged antlered skull of a young adult male IGF 243 (MGUF) of *Cervus nestii* from Figline (Fig. 41) is characterized by the unflexed braincase with flattened parietal bones. The face is very long: the index LF/CBL amounts to 61.2%. The variation range of the LF/CBL index is 58.6 - 61.0% in *C. elaphus elaphus* (n=5), 52.8 - 55.1% in *C. nippon* (n=3), and 52.3 - 56.5% in *Dama dama* (n=13). The projection of the anterior edge of orbit runs down behind M³. The posterior edge of nasal bones does not reach the line connecting the anterior edges of orbits. The nasal bones have a very short contact with ethmoidal openings (shorter

than ½ of the ethmoidal opening length). The preorbital fossae are deep. Pedicels are long and sloped from the face toward the posterior. Frontal bones are flat and just slightly depressed between orbits. The horizontal ramus of mandible forms an open angle (110°) with the ascending mandibular part. The upper canines are present. The angle between labial and lingual walls of upper molars is comparatively narrow and amounts to 30°. The morphology of P₄ is primitive. The lower premolar series attains 64.3% of the molar series length in the specimen IGF 243, falling within the range of variation of modern European red deer (60.3% - 65.2% according to the sample stored in NMNH).

The cranial morphology suggests that *C. nestii* is one of the earliest representative of the *elaphus* group, showing a greater affinity with *C. elaphus* than with *C. nippon*. The remains of *Cervus nestii* are also reported from Olivola (Croitor 2014) and Dmanisi, where it was described as *Cervus abesalomi* Kahlke, 2001 (Croitor 2006a; Bukhsianidze 2016).

CERVUS ELAPHUS LINNAEUS, 1758

C. elaphus acoronatus Beninde, 1937 is the most archaic subspecies of red deer that dispersed in Europe by the beginning of Middle Pleistocene. This is a large-sized form characterized by the advanced molarization of P₄ and the presence of the bez tine as in modern *C. elaphus*. The distal part of antlers is terminated by a simple transversal distal fork as in *C. nestii* and the modern subspecies *C. elaphus bactrianus* Lydekker, 1900 and *C. elaphus yarkandensis* Blanford, 1892. *Cervus reichenau* Kahlke, 1996 (= *Cervus elaphoides* Kahlke, 1960) from the early Middle Pleistocene of Mosbach is based on antler remains of a young individual of red deer and has proved to be a junior synonym of *C. e. acoronatus* (Lister 1990). The proportions of the lower mandible 32863/17 (SMNH) from Mosbach falls within the range variation of modern red deer: the relative length of diastema with respect to lower tooth length is 74.9%; the premolar to molar series length ratio is 61.3%. Measurements of the specimen from Mosbach correspond

to the comparatively moderate for red deer body mass of 170 kg.

C. elaphus angulatus Beninde, 1937 from the Late Middle Pleistocene of Steinheim (250 kyr: Geist 1998) is a direct descent of *C. e. acoronatus* that evolved the most unusual shape of its distal crown. Young individuals evolve the *acoronatus*-type antlers with a simple frontally oriented distal fork, as one can see in the specimen ST-18176 (SMNH). The distal part of fully grown antlers may be variable, however, there is a general and specific morphological pattern: the beam segment above the middle tine is more robust than the beam segment below the middle tine; the antler crown preserves the initial distal fork, but it evolves a very strong and long caudal tine, which forms a

right antler with the beam and directed posteromedially (Fig. 42). This caudal crown tine often is extended into a small horizontal palmation that bears additional tines (up to six). The functional significance of the caudal crown tine is not clear. Possibly, it had the same function as the posterior tine in *M. giganteus* and *R. tarandus* and other deer adapted to the open or/and wet landscapes: the function of removing the flying parasites from the back in rutting males, thus increasing their combat capacities (Croitor 2016). According to Geist (1998), the red deer of the *angulatus*-type survived in the Iberian glacial refugium and a high percentage of the south Spanish deer carry this diagnostic antler form.

Due to its higher biogeographic isolation and the connection with the Balkan Peninsula, Italy has yielded red deer forms different from those of Western Europe. *C. elaphus rianensis* Leonardi & Petronio, 1974 from the Aurelian Age of Middle Pleistocene of Italy is an endemic descent of *C. e. acoronatus* that is also characterized by antlers terminated with a distal fork. This contemporaneous with *C. e. angulatus* form of red deer is distinguished by the diminished body size (male body mass is ca. 130 kg), the relatively short limbs and the conspicuously shortened distal beam segment between the trez tine and the distal fork (Leonardi & Petronio 1974). The somewhat older *C. elaphus eostephanoceros* Di Stefano & Petronio, 1993 from the late Galerian Age of Cava Nera Molinario (Italy), apparently, is a junior synonym of *C. e. rianensis*. The type antler of *C. e. eostephanoceros* is characterized by a shortened distal part above the trez tine as in *C. e. rianensis* (Di Stefano & Petronio 1993: fig. 2).

C. elaphus siciliae Pohlig, 1893 from the end of Middle - Late Pleistocene of Sicily is a slightly smaller deer (ca. 100 – 110 kg) with the specific adaptations to grazing: the facial tubercle zone is particularly rough, the stout and the mandibular diastema

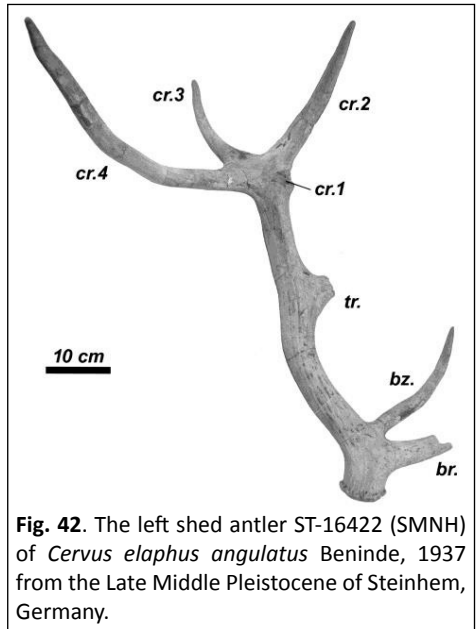


Fig. 42. The left shed antler ST-16422 (SMNH) of *Cervus elaphus angulatus* Beninde, 1937 from the Late Middle Pleistocene of Steinheim, Germany.

are relatively short, the premaxillary bones are broad and squared, the mandibular body is relatively high (Gliozzi et al. 1993). The advanced morphological character is seen in more divergent and short pedicles if compared to modern red deer. Antlers are simplified: in 40% of specimens the bez tine is missing; the trez tine also may be vestigial or even completely absent; the distal part of antler is formed by two or three tines (Gliozzi et al. 1993).

C. elaphus aretinus Azzaroli, 1961 from the last interglacial phase of Val di Chiana (Italy) represents a different dispersal event of red deer. This subspecies is characterized by the absence of bez tine, the long trez tine, and a massive distal crown, which, however, is simple and resembles the *C. elaphus maral* type: the crown is formed by a stronger posterior axial tine and multiple “secondary” tines (up to five) that are inserted on the main crown axis (Azzaroli 1961; Croitor & Cojocar 2016). Another antlered skull with *maral*-like antlers is reported from the Late Pleistocene of Liguria (Le Prince, Italy) (Barral & Simone 1968: 87, fig. 14-1). Obviously, *C. elaphus aretinus* is closely related or may be even synonymous with Caucasian and Caspian red deer *Cervus elaphus maral* Lydekker, 1898. The Balkan-Anatolian-Caucasian glacial refugium is the area of origin and the centre of dispersal of *Cervus elaphus maral* (Sommer et al. 2008; Meiri et al. 2013). Perhaps, *C. elaphus aretinus* entered the Italian Peninsula via the narrow way passing between the Alps and the Dinaric Alps.

The remains of *C. elaphus barbarus* Bennett, 1833 from the Late Pleistocene of Doukkala II (Morocco) is characterised by the advanced molarization of P₄, the missing bez antler tine, and the rather moderate body size similar to that of the coeval Wurmian red deer from Comb Grenal of southwestern France (Laquay 1986). The estimated body mass of a male individual from Doukkala-II amounts to ca. 220 kg according to the dental measurements provided by Laquay (1986). Adult individuals of the modern Barbary stag *C. e. barbarus* are characterised by a primitive type of pelage colour with white spots on the back in adulthood that is regarded by Geist (1988) as a pedomorphic feature. The exact time of dispersal of red deer in Africa is not known. The presence of red deer in north-western Africa is recorded only in Late Pleistocene. Gentry (2010) reported a single cervid molar of an older Pleistocene age from the Nile Valley in Sudan. Finally, Ludt et al. (2003) obtained a surprisingly high genetic differentiation of the modern *C. e. barbarus* from the rest subgroups of the modern red deer with the time of divergence ca. 2.2 Ma that roughly coincides with the dispersal of *Cervus nestii* in the Ponto-Mediterranean Area.

CERVUS CANADENSIS ERXLBEN, 1777

The extremely large basal antler portion from the Late Pleistocene deposits of Kent's Cavern (England) described by Owen (1846) as *Cervus (Strongyloceros) spelaeus* provoked the long-lasting debate on the presence of wapiti (*Cervus canadensis*) in the Late Pleistocene of Europe. The specimen from Kent's Cavern recalls European red deer morphology but with large dimensions approaching to the largest modern North American wapiti antlers. *Cervus strongyloceros* Schreber, 1836 (one of synonyms of *C. canadensis* Erxleben) is the type species of *Strongyloceros* Owen, 1846. Lydekker

(1915) regarded *Strongyloceros* as a junior synonym of *Cervus* and this viewpoint was generally followed since then. By the end of XIX century, several reports on the presence of large fossil wapiti-like deer in Europe appeared in the scientific literature (see, for instance, Belgrand 1883: Pl. 22, fig. 1). However, De Stefano (1911), considered that the presence of *Cervus canadensis* in Europe based on poor osteological remains cannot be regarded as proven. The analysis of mitochondrial DNA of some elaphine deer remains from Kent's Cavern revealed that they belong to European red deer *Cervus elaphus* (Meiri et al. 2013), therefore the question on the presence of wapiti in the fauna from Kent's Cavern remains open. Nonetheless, the occurrence of wapiti in South-Eastern Europe was recently attested by the analysis of mitochondrial DNA sequences from Late Pleistocene remains of elaphine deer from the Emine-Bair-Khosar Cave in Crimea, Ukraine (Stankovic et al. 2011). The absolute age of the specimens in question is $33,100 \pm 400$ BP and $42,000 \pm 1200$ BP (*ibidem*). The mitochondrial DNA extracted from large elaphine deer remains discovered in the Peștera cu Oase site (MIS 3, Romania) indicate clearly that the Romanian sample falls within the "wapitoid" clade (Parfitt & Lister 2013).

The presence of *C. canadensis* in the Late Pleistocene of Europe is confirmed by the finding of the antler fragments from the upper layer of Paleolithic site of Climăuți II (Moldova) dated to $20\,350 \pm 230$ y. BP (Croitor & Obada, in press). The antler fragments from Climăuți II are exceptionally large in comparison to those of modern red deer and, what is most important, one of the specimens is a distal part of antler that represents a comb-like morphological pattern of crown shape typical for *Cervus canadensis*. The antler crown consists of three tines that are situated almost in the same plane (more or less parasagittal with respect to the animal's main body axis). Perhaps, the remains of *C. canadensis* are more frequent in the Late Pleistocene of Europe, but they in most cases are misunderstood, since the details of craniodental morphology of this species are little known. One of such specimens 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). Unlike *P. solilhacus*, the mandible 2003-4-420-SOL is characterized by a very long diastema, which attains 82.6 % of the lower tooth row length, slightly exceeding the proportions of lower mandible to the maximal value of modern red deer (the ratio of diastema length to lower tooth row length varies between 63.0% and 82.5% in the sample stored in MNHN, n=10). The diastema in a slightly larger mandible 2003-4-439-SOL ascribed to *P. solilhacus* is relatively shorted and amounts to 67.2%. P_4 in the specimen under discussion is not fully molarized: paracone and metacone get in touch, but are not fused. The premolar/molar ratio is 60.4%. The body mass estimation based on the dental measurements of the mandible 2003-4-420-SOL is 350 kg.

Table 3. Measurements of mandibles of large-sized deer (mm).

| Species | <i>Cervus canadensis</i> | <i>Praemegaceros solilhacus</i> | <i>Praemegaceros pliotarandoides</i> | <i>Arvernoceros cf. verestchagini</i> | <i>Arvernoceros sp.</i> | <i>Eucladoceros dicranios</i> |
|------------------------------------|--------------------------|---------------------------------|--------------------------------------|---------------------------------------|-------------------------|-------------------------------|
| Site | Soleilhac | Soleilhac | Apollonia-1 | Apollonia-1 | Liventsovka | Liventsovka |
| Collection number | 2003-4-420-SOL | 2003-4-439-SOL | APL-402 (sin) | APL-384 | LIV-836-1810/3 | LIV-604-1801/9 |
| L P ₂ -M ₃ | 151.8 | 156.3 | 176.0 | 188.0 | 143.8 | 119.0 |
| L P ₂ -P ₄ | 57.0 | 61.3 | 68.7 | 73.3 | 55.0 | 47.6 |
| L M ₁ -M ₃ | 94.3 | 98.8 | 103.0 | 116.4 | 90.0 | 73.1 |
| L mandible | | ≈380.0 | | | | |
| L diastema | 125.0 | 105.0 | | ≈ 95.0 | 102.1 | |
| L P ₂ - for. ment. | 74.0 | 48.5 | 52.0 | 72.5 | 55.0 | 44.0 |
| H diastema | 25.3 | 21.2 | 22.5 | 23.8 | 22.6 | 16.7 |
| H / P ₂ | 47.7 | 43.3 | | 37.7 | 34.6 | 27.8 |
| H / M ₁ | 48.5 | 50.6 | | 43.1 | 41.3 | 33.3 |
| H / M ₂ -M ₃ | 51.0 | 54.0 | | 50.7 | 45.6 | 38.2 |
| D / P ₂ | 17.6 | 17.2 | | 16.5 | 14.2 | 12.5 |
| D / M ₁ | 27.3 | 26.5 | 19,9 | 25.4 | 20.5 | 17.4 |
| D / M ₂ -M ₃ | 31.3 | 29.8 | 23.4 | 28.1 | 23.2 | 20.6 |

Cervus canadensis palmidactyloceros De Stefano, 1911 is an endemic Late Pleistocene wapiti from the Italian Peninsula characterized by a typical for wapiti large body size (CBL = ca. 430 mm) and the palmated antlers. This cervid form entered the Italian Peninsula during the Last Glacial Maximum and became extinct after the cold phase of Younger Dryas (Croitor & Obada, in press).

Genus *Megaloceros* Brookes, 1828

According to the traditional broad understanding of *Megaloceros*, the genus includes all giant Cervinae forms from Western Eurasia, as well as their supposed smaller forerunners and dwarfed insular descendants (Azzaroli 1953, 1979; Lister 1994). At present moment, the traditional concept of *Megaloceros* is rejected, since the group of giant deer is rather represented by several independent lineages that share the similar eco-morphological features, but phylogenetically are quite distant one from another (Vislobokova 1990, 2012; Croitor 2006b). *Megaloceros* is distinguished from other large-sized deer by its concave frontal bones, circular cross-section of pedicles, comparatively long and little flexed braincase, rather short orbitofrontal portion of skull (the anterior edge of orbit is situated above M³), and the remarkable cranial pachyostosis, which is expressed in the strong thickening of mandible, the thick cranial bones, the early and complete obliteration of cranial articulations, the ossified vomer, and the small or even closed ethmoidal orifices. Upper canines are not present. P₄ is molarized.

The systematic position of giant deer was a subject of long lasting debates. Lydekker (1898) included *M. giganteus* in the so-called “Damine groupe” and suggested its close relationship to the modern fallow deer. This viewpoint was supported by Geist (1998).

Lönnerberg (1906) noticed the completely ossified vomer, which completely divides the posterior nares into two separated passages. This peculiar cranial character, as well as the flattened basal tine where regarded by Lönnerberg (1906) as arguments for the close phylogenetic relationship between *M. giganteus* and reindeer *Rangifer tarandus*. Lister (1994) noticed that the vomerine septum in giant deer does not completely divide the nasal cavity as in Capreolinae, but only in its anterodorsal part, as in Cervinae. Lister (1994) assumes that the ancestry of *M. giganteus* may lie close to *Praemegaceros verticornis* or *Praedama savini*, but, as he acknowledges, this relationship has not been demonstrated. Heintz (1970) suggested that *M. giganteus* could be a direct descent of *Arvernoceros ardei* from Western Europe. This assumption was based on the flattened shape of first tine, the presence of small distal palmation, and the upper molars with cingulum which were ascribed to *A. ardei*. Vislobokova (1990, 2009, 2012) followed Heintz's (1970) point of view and assumed the origin of both *Arvernoceros* and *Megaloceros* from the Late Miocene Asian *Praesinomegaceros*, which is believed to be a transitional form between *Cervavitus* from one hand and *Sinomegaceros* with *Arvernoceros* from another hand.

Molecular phylogenetic studies has revealed that the fallow deer is the closest extant cervid species to *M. giganteus*, although the evolutionary divergence between *Megaloceros* and *Dama* has occurred very early, 4–5 Myr (Lister et al. 2005) or even 10.7 Myr (Hughes et al. 2006). The close phylogenetical relationship between *M. giganteus* and *D. dama* is also supported by the some shared characteristics of the cranial morphology: both species show a relatively long braincase, long nasal bones (synapomorphy), a relatively short orbito-frontal portion of skull, absent upper canines, and a similar shape of the broadened basioccipital at the level of the pharyngeal tuberosities. Unlike *Dama*, *Megaloceros* maintains the primitive unflexed shape of braincase.

MEGALOCEROS GIGANTEUS (BLUMENBACH, 1799)

Van der Made (2006) has already pointed out that the taxonomy of giant deer is still unclear and its type material and type locality remain unknown. Blumenbach (1799: 697) for the first time applied the species name *Alce gigantea* mentioning the fossil remains from Ireland and quoting the immense size of giant deer skull and antlers (the reported distance between summits of antlers is 14 feet, or ca. 4.3 m), however, without any explicit reference to a certain publication or collection. The first detailed description of the giant deer from Ireland was published by Molyneux (1697) shortly before Blumenbach (1799) proposed the scientific name for the giant deer of Ireland. Molyneux (1697) provided measurements and a figure of an antlered skull from Dardistown near Drogheda (Ireland), but apparently, this is not the specimen that Blumenbach was keeping in his mind. The span of antlers of the specimen from Dardistown reported by Molyneux (1697) is only 10 feet 10 inches (ca. 3.3 m), distinctly less than the antler span mentioned in the brief Blumenbach's (1799) description. It is difficult or may be even impossible now to identify the fossil material that Blumenbach (1799) referred to. The large palmated antlers of the giant deer from Ireland are

directed sideward, with a small basal bifurcated tine, an anterior and a posterior tines that are not coalesced with distal palmation, and crown tines situated on the distal and anterior margins of the palmation.

The Irish sample is characterized by very small or almost completely closed ethmoidal openings (most probably, the side effect of cranial pachyostosis). Preorbital pits are small, may be very shallow or clearly expressed, quite deep. Possibly, the broad variability in the degree of development of preorbital pits is due to the mixed character of material. The nasal bones are extended far behind the line connecting the anterior edges of orbits. The orbitofrontal part of the skull is rather short: the anterior edge of orbit is situated above M^2 . Parietal bones are quite flattened, the braincase is little flexed. The basioccipitale is broad, pentagonal, broadened in pharyngeal tuberosities. Foramina ovale are very small. The nasopremaxillary articulation is very long. The upper molars are supplemented with a strong cingulum. The horizontal ramus of mandible is more or less thick, showing a various degree of pachyostosis. The mandibular pachyostosis may be a dimorphic character stronger expressed in males (Lister 1994). The premolar/molar ratio varies between 53.6% and 61.1%. P_4 is always molarized.

Vislobokova (2012) regards the giant deer from Ireland as a nominotypic subspecies *Megaloceros giganteus giganteus* and reports the fossil material from Ireland as a “type population of subspecies”. However, the sample of giant deer from Ireland stored in various museums of Europe, apparently, does not represent a single population. The material from Ireland shows a significant and meaningful split in metacarpal length and robustness. The metacarpals of mounted skeletons of the female exposed in the Paleontological Gallery of Paris, the male from the Natural History Museum “Grigore Antipa” of Bucharest, the male from Athlone (Ireland), the male from an unidentified Irish site exposed in the Museum of Nature of Wroclaw, and the skeleton from Enniscorthy (Ireland; stored in the Sedgwick Museum of Cambridge) described by Reynolds (1929) are short and relatively robust, overlapping with the sample from Bruine Bank (Croitor et al. 2014). The metacarpals of the mounted male skeletons from the Paleontological Gallery of Paris and the Paleontological Institute of Munich are particularly long approaching the giant deer from Schlutup (Germany) and Sapozhok (Russia). This group of specimens corresponds to van der Made’s (2006) Late Devensian group of “intermediate type of metapodials”. Regarding the relative length of upper premolar series, the sample from Ireland again is divided in two groups: the small group of specimens with relatively long premolar series that overlap with the main part of sample from Rhine basin, North Kazakhstan, and the specimen from Brînzani-1 (Moldova), and the group with relatively short premolar series that may be approached to the larger specimen from Sapozhok (Croitor et al. 2014). It is difficult to confirm the relationship between the limb proportions and the tooth series proportions taking in consideration only the mounted skeletons of giant deer from Ireland, since those showpieces originally were subjects of commercial selling and we don’t know if the skeletons are genuinely articulated, or (what is more probably) compiled. Therefore, it is very difficult to define a “typical Irish” subspecies *M. giganteus giganteus*, since the material from Ireland includes both the “robust” and “long-limbed” types of giant

deer. Van der Made (2006) and Lister (1994) regarded the “typical” giant deer from Ireland as one of the most long-limbed form. According to van der Made (2006), the relatively slender Irish form of giant deer arrived in Western Europe 10-13 Ka from Eastern Europe.

The skeleton of giant deer from Sapozhok (Ryazan, Russia) stored in the Paleontological Institute, Moscow (collection number PIN-337) is a genuinely articulated skeleton that is important for our understanding of the Irish material. This is a long-limbed large form characterized by the antler shape as in *M. giganteus* from Ireland, the well-developed cingulum in upper molars, and the particularly short premolar series, thus suggesting the association of long limbs with short premolar series (Croitor et al. 2014). The presence of large long-limbed giant deer with advanced dentition in Eastern Europe supports the hypothesis of van der Made (2006) on immigration of “classical Irish” form of *Megaloceros giganteus* from the East around 13 ka. The older remains of giant deer are described as several subspecies distinguished mostly by their antler morphology.

Megaloceros giganteus antecessens Berckhemer, 1941 from the Holsteinian of Steinheim, Germany (ca. 400 or 300 kyr BP), is the oldest giant deer form in Europe that is considered as a primitive forerunner of *M. giganteus ruffii* and *M. giganteus giganteus* (Azzaroli 1953; van der Made 2003; Vislobokova 2012). Azzaroli (1953) granted to Berckhemer’s giant deer the full specific rank because of the remarkable shape of its antlers. The antlers of *M. giganteus antecessens* are most deviant if the Irish giant deer is regarded as a “typical” form: the basal tine in the deer from Steinheim is transformed into a broad plate-shaped palmation, the middle tine adjoined the distal antler palmation, the crown tines are inserted on anterior and distal sides of palmation, while the posterior tine is very large and flat, therefore the general shape of distal part of antler is rather elk-like. Kahlke (1999) noticed a conspicuous morphological affinity of *M. giganteus antecessens* with *Sinomegaceros pachyosteus* from Zhoukoudian and explained this affinity as a morphological parallelism in similar ecological circumstances. This subspecies is characterized by the long nasal bones that extend behind the anterior orbital line, the small but clearly visible preorbital fossae, and elongated distal portions of limbs. The lingual cingulum in upper molars is not developed.

Megaloceros giganteus ruffii Nehring, 1891 from Kottbus area (Germany) characterized by the smaller antler span, the broader palmation and the crown tines inserted on the distal edge of the palmation (not on the anterior side as in Irish giant deer). The antlered skull Nr. 6517.5.9.73.4 from Bruhl (SMNH) ascribed to this subspecies (Vislobokova 2012) is characterized by rather large and deep preorbital fossae, closed ethmoidal orifices, smooth and irregularly rounded *bullae tympani*, and protruding orbits. The cingulum in upper molars is not developed.

Megaloceros giganteus germaniae Pohlig, 1892 is characterized by a more compact antler crown, a frontal orientation of palmations, which apparently become more visible during the frontal visual contact of their bearer with a rival. Its antler crowns are strongly bent medially and toward the posterior, the middle tine normally is separated from the palmation.

Megaloceros giganteus italiae Pohlig, 1892 is generally characterized by the similar type of antler shape, as *M. giganteus ruffii* and *M. giganteus germaniae*, however, its medial tine often adjoins the distal palmation (Pohlig 1892). According to van der Made (2006) and Vislobokova (2012), the subspecies names *ruffii*, *germaniae* and *italiae* are synonymous. Possibly, the Italian giant deer should be maintained as a separate subspecies, since the antlered skull IGF11630 (MGUF) is very distinct from the Irish, German, and East European samples in its relatively broad braincase: the index DNr/LBr in the skull from Tuscany is 129.9%, while in the lumped data for Irish and German samples varies between 85.4% and 101.1% (Croitor, work in progress).

Van der Made (2006) distinguished in the sample from the Rhine basin and North Sea two morphological forms of giant deer: the older Holsteinian/Hoxnian and Saalian/Wolstonian *M. giganteus* “*antecedents/germaniae*” with slender metacarpals, and younger Eemian *M. giganteus* *ssp.* with robust metacarpals. The majority of findings from Poland, Ukraine, and Moldova belong to the giant deer form characterized by the relatively long upper and lower premolar series, the very weak or missing cingulum in upper molars, and, apparently, represent the “robust type” described by Lister (1994) and van der Made (2006). The giant deer from Biśnik Cave (70–60 ky BP; Poland) seems to be close to *M. giganteus ruffii*, but the definite conclusion is not possible, since antlers of the Polish form are not known. The female skull of the giant deer from Biśnik Cave is characterized by the shallow, but clearly outlined preorbital fossae (their depth is 5.5 mm), the short nasal bones that do not reach the imaginary line connecting the anterior edges of orbits, the weak development of cingulum in upper molars, and the rather short massive metacarpus, which is somewhat smaller than the metacarpal bone found in the association with the type specimen of *M. giganteus ruffii* (Croitor et al. 2014). It is difficult to classify the shape of metacarpal from Biśnik as robust or slender, since it is characterized by relatively narrow distal epiphysis and rather massive shaft. The lower mandibles from Biśnik are characterized by the relatively long premolar series (61.9–65.6%, n=3) and stand closer to large individuals of the sample from the Rhine Basin stored in SMNH.

MEGALOCEROS MUGHARENSIS (DI STEFANO, 1996)

The remains of this peculiar large-medium sized deer are very fragmentary, but interesting: antlers are characterized by a strong bifurcated flattened basal tine situated close to the burr. The angle between the basal tine and the beam is very obtuse. The proximal portion of antler beam is flattened; a variable in shape middle tine is situated at 10–15 cm from the burr (Di Stefano 1996). Di Stefano (1996) described *Dama clactoniana mugharensis* from the Middle Pleistocene of Tabun E, Middle East, as a transitional form between *Dama clactoniana* from the Middle Pleistocene of Europe and modern *Dama mesopotamica*. This assumption is hardly probable, since *D. clactoniana* is characterised by a simple cylinder-shaped basal tine and never develops flattened bifurcated variants of the basal tine, although supernumerary and even bifurcated crown and middle tines are common in this species (Leonardi & Petronio 1976). The antlers of *D. mesopotamica* are characterized by the significantly reduced

size of the basal tine, therefore showing the direction of the evolutionary specialization quite opposite to the condition seen in *M. mugharensis*. The flattened bifurcated basal tine situated very close to the burr and the obtuse angle of the first ramification, in my opinion, approach the cervid from Tabun to *M. giganteus*. Di Stefano (1996) also reports a comparatively strong development of basal structures in upper molars (entostyle and the “anterior and posterior cingulum”) that correspond to the frequent development of cingulum in *M. giganteus*. The lower premolar series seems to be relatively long (66%, measured from the photographs in Di Stefano 1996) and represents a primitive condition similar to the primitive form of *M. giganteus* from Rhine Bassin. The systematic significance of the long premolar series in this case becomes important in the combination with antler morphology. The relative length of premolar series in the deer from Tabun is more primitive than that of *Dama clactoniana* from Riano (the premolar/molar index is 58.3%) and is still more primitive than Early Pleistocene *Dama vallonetensis* from Capena (the premolar/molar index is 58.1%) and Pirro Nord (56.8%). Therefore, the relatively long premolar series of *M. mugharensis* rules out the close relationship between this deer and the Pleistocene fallow deer. Limb bones are reported to be squat (radius length is ca. 215–220 mm and mid-shaft breadth is ca. 29 mm; Di Stefano 1996: fig. 8) that may be regarded as an indication to the body size reduction similar to that of *C. elaphus rianensis*. Taking into account the enlisted characteristics, one can assume that the medium-sized cervid from the Near East is a primitive or dwarfed form of giant deer *Megaloceros mugharensis* (Di Stefano, 1996). One can assume that *M. mugharensis* together with *M. giganteus antecessens* belongs to the earliest dispersal event of giant deer into Western Palearctic.

Genus *Megacerooides* Joleaud, 1914

Joleaud (1914) created the subgenus *Megacerooides* within the genus *Cervus* for an endemic odd cervid *Cervus algericus* Lydekker, 1890 (= *Cervus pachygenys* Pomel, 1893) from North Africa in order to underline its assumed archaic character and transitional systematic position between *Megaloceros* and *Dama*. Arambourg (1932, 1938) reported some new important findings of cervid cranial remains from the Late Pleistocene of Algeria (Guyotville) and Morocco (Ain Tit Mellil) that permitted him to elevate *Megacerooides* to the genus level. Joleaud (1914) stressed the affinity between *M. algericus* and the European giant deer, assuming for the African form an intermediate position between *Megaloceros* and *Dama*. Azzaroli (1953) divided all giant deer in two phylogenetic branches: the “*Megaceros giganteus* group”, which also included Asian *Sinomegaceros* regarded as the terminal evolutionary branch of this group, and the “*Megaceros verticornis* group” with *M. algericus* associated with “*M. verticornis* and other related forms. Ambrosetti (1967) gave the formal taxonomical status to Azzaroli’s informal groups: he divided the genus *Megaceros* Owen, 1843 (junior synonym of *Megaloceros* Brookes, 1828) into subgenera *Megaceros* (Azzaroli’s “*giganteus* group”), and *Megacerooides* (“*verticornis* group”). The assumed close phylogenetic relationship between *Megacerooides algericus* and *Praemegaceros verticornis* actually was based on a single morphological character: the flattened frontal bones (Azzaroli 1953, 1979; Ambrosetti 1967). The detailed study of cranial and dental

morphology of *Megaceroides algericus* revealed its deep evolutionary specialization and the significant morphological and phylogenetic remoteness from *Praemegaceros verticornis* and other allied *Praemegaceros* forms (Croitor 2004, 2006b).

MEGACEROIDES ALGERICUS (LYDEKKER, 1890)

The cranial morphology of *M. algericus* is atypical and have no analogues among Cervidae (Fig. 43). The skull is very broad, while the length proportions of the cranium are modified insignificantly; the skull breadth attains more than 60% of condylobasal length. Splanchnocranium is relatively short: the length measured from the anterior edge of orbits to prosthion makes is shorter than 1/2 of condylobasal length. The position of *bregma* between the posterior edges of pedicles and the position of *nasion* slightly caudally with respect to anterior edges of eye sockets are similar to the morphological condition found in *M. giganteus*. The cranial bones are very thick, reminding the cranial hyperostosis described in *Megaloceros*. However, unlike in *Megaloceros*, the vomer apparently is not affected by hyperossification. The zygomatic arches are markedly thin and feeble, contrasting with overall robustness of the skull. The braincase is moderately flexed: the angle between parietal bones and face profile amounts to ca. 135° and shows an intermediate condition between *Dama* and *Megaloceros*. The parietal bones are flat. The pedicles are rather long, set obliquely on the skull and some-what deflected toward the rear and the sides. The pedicles are slightly compressed in the anteroposterior direction, however this compression is not as strong as in the advanced species of *Praemegaceros* (*P. verticornis*, *P. dawkinsi*, and *P. solilhacus*). The frontal bones are very broad (corresponding to the disproportionately

broad skull), flat and slightly depressed from the both sides of the frontal suture. The ethmoidal orifices are completely closed. The preorbital fossae are not developed. The nasal bones are relatively narrow and rather long, extending behind the imaginary line connecting the anterior edges of orbits, as in *Megaloceros* and *Dama dama* (but not as in *Dama clactoniana*). The orbito-frontal portion of cranium is rather short, as in *Dama* and *Megaloceros*: the anterior edge of orbit is situated above the M²-M³ border. The eye sockets are relatively large, as in *Dama*. The basioccipitale is broad and bell-shaped. The *bullae tympani* are rather large, rounded, projecting outside (as in *Dama*), compressed in the medio-lateral direction. The anterior bony thorn of *bullae tympani* is not present in *Megaceroides*, unlike some Cervinae (*Cervus*, *Rucervus*). The relative length of upper tooth row with respect to

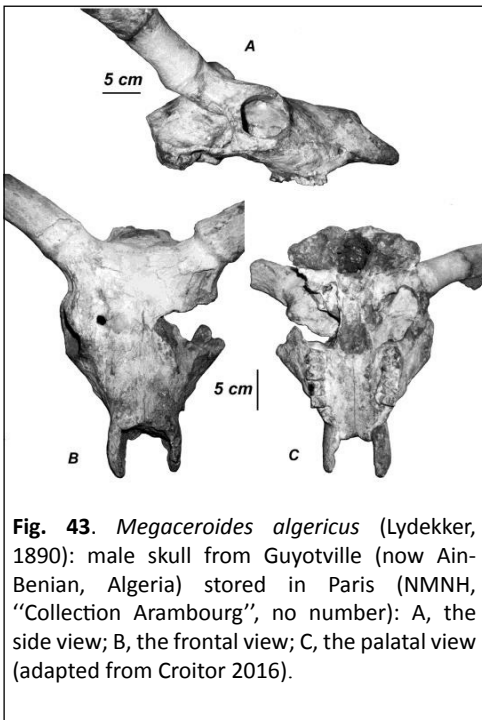


Fig. 43. *Megaceroides algericus* (Lydekker, 1890): male skull from Guyotville (now Ain-Benian, Algeria) stored in Paris (NMNH, "Collection Arambourg", no number): A, the side view; B, the frontal view; C, the palatal view (adapted from Croitor 2016).

the basal length of skull amounts to 29.5%, being fairly close to the ratio found in *Megaloceros*, *Axis* and *Dama*. Nonetheless, the displaced toward the anterior position of upper cheek tooth row represents a specific character of *M. algericus*. The diastemal part of mandible is very short. The anterior portion of mandible from M_1 to symphysis has a cylindrical shape (Fig. 44). Behind M_1 , the mandible became higher and more robust. The lower tooth row is displaced orally due to the very short diastema and obliquely set ascending portion of mandible. The mandibular pachyostosis appears very early during the ontogenetic development and is recorded even in juvenile individuals with deciduous teeth, although the juvenile mandible is less thick than the mature specimens (Croitor 2016).

Upper canines are missing. Cheek teeth are relatively small. Lower fourth premolar (P_4) is molarized: its metaconid is fused with paraconid. The premolar series is comparatively short, however, a broad variation is observed here. The premolar/molar length ratio amounts to 60.5% in the mandible FIL166, while the same tooth series ratio in the two specimens from Phacochoeres amounts to 45.0% and 52.9% (Hadjouis 1990). The lingual side of P^4 is not split into protocone and hypocone, not even grooved. The relative size of upper third molar is visibly reduced; therefore M^2 is noticeably larger than M^3 . The angle between labial and lingual walls of upper molars amounts to 37° , as in *Dama dama*. The hypoconal fold is present only in M^3 . Two small enamel folds are found on the external side of anterior hypoconal wing in M^2 . Unlike the holotype of *M. algericus* from Hammam Meskoutin, the additional material discovered by Arambourg (1932, 1938) represents a deer from with some-what smaller upper cheek teeth (length of M^1 - M^3 tooth series amounts to 54.1 mm in the specimen from Guyotville against 58.5 mm in the holotype of *M. algericus*). The cingulum in upper molars seems to be a variable character: it is well-developed in the type specimen from Hammam Meskoutin and is not developed in Arambourg's specimen. It is necessary to mention, that the type from Hammam Meskoutin does not show the specific size reduction of M^3 . Possibly, the observed morphological differences may have a taxonomical significance at species or subspecies level, but the available data are insufficient. However, if this is the case, one can distinguish two chronological forms of the endemic North African deer: an older larger form from Hammam Meskoutin with strong cingulum and normally developed M^3 , and a more specialized descent form with smaller dentition, reduced cingulum and marked reduction of M^3 . If this is true, I would advise to use the Pomel's name proposed for the African cervid form with pachyostotic mandibles and upper molars without cingulum as a subspecies *Megacerooides algericus pachygenis* (Pomel, 1892). In this case, the lower mandible, the isolated upper molar, the radius, and fragments of antlers from Berrouaghia (Algeria) figured by Pomel (1892: pl. VII-VIII) should be regarded as syntypes.

The complete antlers of *Megacerooides algericus* are unknown. The available material shows that the antlers are normally developed and do not show any sign of "degeneration" reported by Azzaroli (1979). Antlers are terminated with a palmation. The proximal part of antler beam has a circular transversal section and lacks basal tines. The tine inserted on the anterior side of the beam (homologous with the middle tine in

Megaloceros giganteus) is situated from the burr at a distance ca. two times exceeding the diameter of antler base (Hadjouis 1990; Croitor 2016).

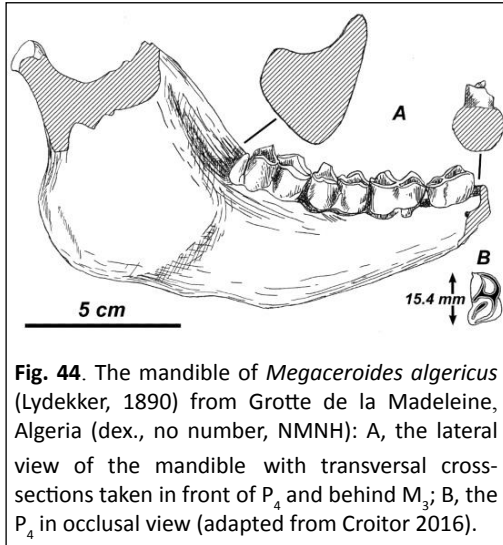


Fig. 44. The mandible of *Megaceroides algericus* (Lydekker, 1890) from Grotte de la Madeleine, Algeria (dex., no number, NMNH): A, the lateral view of the mandible with transversal cross-sections taken in front of P_4 and behind M_3 ; B, the P_4 in occlusal view (adapted from Croitor 2016).

Unlike *Praemegaceros*, *Megaceroides* is characterized by the relatively longer braincase (a primitive character), the cylinder-shaped pedicles (not compressed anteroposteriorly or dorsoventrally as in some advanced species of *Praemegaceros*), the cranial and mandibular pachyostosis, and the long nasal bones (Croitor 2006b, 2016). *Megaceroides* shares with *Dama* the broad bell-shaped basioccipitale, the large orbits, the large rounded *bullae tympani*, the flexed braincase, the missing upper canines, and the similar proportions of lower tooth row. However, the shape and relative length of the braincase, the position of the antler pedicles, the

developed cingula in upper molars, and the cranial hyperostosis of *M. algericus* suggest its greater affinity with *M. giganteus* (Lydekker 1890; Joleaud 1914, 1916; Croitor 2016).

The known geo-chronological range of *M. algericus* includes Late Pleistocene–Holocene (ca. 24000 – 6641-6009 ka) (Fernandez et al. 2015) and the fossil record revealing the dispersal of *Megaceroides* into North Africa is not available yet. The origin of *M. algericus* is an important paleobiogeographic question, since it concerns the debated problem on ways of faunal dispersals and exchanges between Africa and Europe during Pleistocene. Joleaud (1916) and Fernandez et al. (2015) assumed that *M. algericus* dispersed into Northern Africa through the Strait of Gibraltar. According to Thomas (1979), the most plausible migration path for African deer is the “Libyan-Egyptian” way, i.e., via the south and southeast coast of the Mediterranean Sea. The opinion of Thomas (1970) is confirmed by the presence of the medium-sized *Megaloceros mugarensis* (Di Stefano, 1996) in the Middle Pleistocene of Near East that seems to be the most probable forerunner of *Megaceroides algericus* and the linking form between *Megaloceros giganteus* and *Megaceroides algericus* (Croitor 2016).

Genus *Dama* Frisch, 1775

The modern fallow deer (*Dama dama*) is characterized by the most advanced cranial morphology among Cervinae: the braincase is much more flexed than in the most of the Old World deer; the parietal bones are convex; the pedicles are short and set vertically on the skull; the basioccipitale is broad in pharyngeal tuberosities, bell-shaped; the *bullae tympani* are very large, smooth, and inflated; the orbits are very large; the orbitofrontal portion is short, so the anterior edges of the orbits are shifted forward and situated above M^2 (also because the orbits are relatively large); the ethmoidal openings are very large and bordered by nasal bones on more than $\frac{1}{2}$ of their length; the upper

canines are missing, P_4 is molarized (Flerov 1952; Croitor 2006a). The angle between axae of neurocranium and splanchnocranium in *Dama dama* amounts to 120° , while in *Axis axis* and *Rucervus duvaucelii* this angle is around 130° (measurements are made on the specimens stored in NHMF). The premolar/molar ratio varies from 46.0% to 61.6% (based on the samples stored in NHML and NHMF, $n=10$). Groves & Grubb (2011) suggest that cranially *Rucervus* resembles *Dama*. Actually, *Dama* is more advanced than *Rucervus* in flexed braincase, short nasopraemaxillary articulation, long extended backward nasal bones, and short vertically set pedicles. The origin of the genus *Dama* remains unclear. Di Stefano & Petronio (2002) consider that *Dama clactoniana* evolved from the “European forms of *Rusa*” (“*Rusa rhenana*”, = *Metacervocerus rhenanus*). Since the cranial morphology of *Dama* in many respects is more advanced than in *Metacervocerus*, it is difficult to confirm or to reject the assumption of Di Stefano & Petronio (2002).

DAMA EURYGONOS AZZAROLI, 1947

This small-sized cervid (the estimated body mass is ca. 70-80 kg) from the Late Villafranchian of Upper Valdarno (Italy) originally was described by Azzaroli (1947) as *Dama nestii eurygonos*. It was distinguished from *D. nestii nestii* (here is regarded as *Cervus nestii*) by somewhat more robust antlers with an obtuse basal ramification and the parasagittal orientation of the distal fork. Azzaroli (1947) assumed the evolutionary relationship of the small deer from Upper Valdarno with the living fallow deer. Later, Azzaroli (1992) created the genus *Pseudodama*, since, according to his opinion, the close affinity of small Villafranchian deer with *Dama* was not demonstrated. Croitor (2006a) elevated *Dama eurygonos* to the species level and suggested its close relationship with modern fallow deer. Pfeiffer (1999) and Petronio et al. (2013) regard the species under study as a primitive deer of the genus *Axis*. Finally, the bony labyrinth analysis carried out by Mennecart et al. (2017) confirmed the close phylogenetic relationship between *D. eurygonos* and modern *D. dama*.

The antlered frontlet IGF245 (MGUF) of an adult male is the holotype of *D. eurygonos* (Fig. 45). Its frontal breadth amounts to 105.5 mm (*D. dama*: 104.4 - 91.8 mm; $n=9$); the breadth of skull behind pedicles is 89.5 mm (*D. dama*: 86.4 - 74.4 mm; $n=9$). The antlers are simple, comparatively robust and four-pointed. Nonetheless, the antler bauplan is typical for *Dama*: the first (basal) tine is strong and forms with the antler beam a very obtuse angle (ca. 120°) at a short distance from the burr; the distal fork is oriented in the parasagittal plan and is formed by a

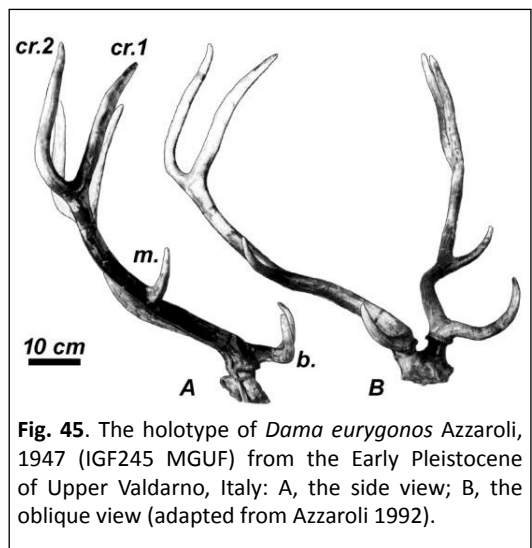


Fig. 45. The holotype of *Dama eurygonos* Azzaroli, 1947 (IGF245 MGUF) from the Early Pleistocene of Upper Valdarno, Italy: A, the side view; B, the oblique view (adapted from Azzaroli 1992).

longer anterior tine that is a continuation of the beam, and the posterior crown tine implanted on the posterior side of the beam. The antlers of modern fallow deer are palmated, however the antler palmation in *D. dama* results from the fusion of multiple posterior tines, therefore the posterior insertion of crown tines represents a typical for *Dama* antler bauplan (Fig. 46, A). The second (middle) tine is rather small in the type specimen and may be missing in younger individuals (Croitor 2006a). The cross-section of beam is circular. The beam segment between the basal and the middle tines and the beam segment between the middle tine and the distal fork are almost of equal length, so the second tine is in more proximal position if compared to *Cervus nestii*.

The damaged skull IGF 244 (MGUF) of *D. eurygonos* from Tasso already shows the typical for *Dama* morphology: the flexed, short and domed braincase, the convex frontal and parietal bones, the short pedicles in vertical position, the relatively large orbits, the short orbitofrontal portion of skull (the anterior edge of orbit reaches the level of M²), the large ethmoidal openings. Unlike modern *D. dama*, the posterior edge of nasal bones does not reach behind the line connecting the anterior edges of eye sockets. The preorbital fossae are large and deep with sharply outlined edges. P₄ seems to be always molarized; upper molars are more brachiodontous if compared to *C. nestii*: the angle between the lingual and labial walls of M² amounts to 37°.

The species is absent in the Olivola F. U. and its first arrival on the Italian peninsula is recorded in the Tasso F. U. (Croitor 2014). The similar to *D. eurygonos* proximal part of antler Nr. 26/20 (IZC) was found in the Villafranchian deposits of Slobozia Mare, South Moldova (Croitor 2006a).

DAMA VALLONNETENSIS (DE LUMLEY, KAHLKE, MOIGNE & MOULLE, 1988)

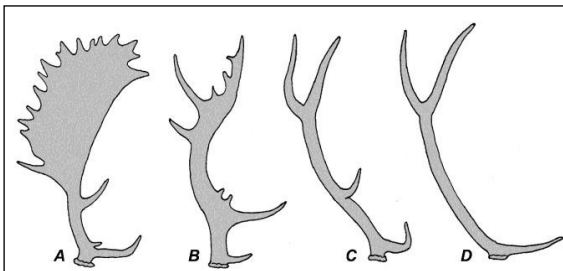


Fig. 46. Variation of antler shape in fallow deer species: A, *Dama dama*; B, *Dama mesopotamica*; C, *Dama eurygonos*, D. *Dama vallonnetensis*.

The body size of this species is intermediary between *D. dama* and *D. clactoniana* (Croitor 2006a). The type specimen is a poor basal fragment of left shed antler Nr. 10170, MPRM (De Lumley et al. 1988: 179, fig. 14) from the Latest Villafranchian of Vallonnet (Alpes Maritimes, France). It is characterized by a very strong and massive basal tine situated very close to the burr and forms a very obtuse angle with the antler beam.

The antler beam is set obliquely with respect to the burr and is directed backward and sideward. The difference between the type specimens of *D. vallonnetensis* and *D. eurygonos* concerns the position of basal tine, which rests directly on the burr in the former species and is mounted at a certain distance from burr in the latter one.

The sample from Vallonnet consists mainly of isolated teeth, fragments of mandibles and several antler fragments. Some dental remains may be ascribed to *D. vallonnetensis* with a certain confidence. M³ Nr. 1174 (RMPPM) is characterised by a moderately oblique lingual wall that forms with the labial wall of the tooth an angle of 37° as in *D. eurygonos*. The additional enamel folds and cingulum are absent. The fragment of left hemimandible Nr. 7879 (RMPPM) is characterized by a molarized P₄ and a rather long premolar series (61.9 % of the molar series length; L P₂-P₃ = 94.5 mm; L P₂-P₄ = 36.3 mm; L M₁-M₃ = 58.6 mm), which is close to the upper limits of relative premolar length in modern *D. dama* (46.0-61.6 %).

The articulated skeleton of adult *D. vallonnetensis* with antlers was reported by Petronio (1979) from the terminal Villafranchian of Capena (Italy) as *Dama nestii eurygonos* brings specific morphological details of the distal portion of antler. The antlers from Capena (Fig. 46, D) are characterized by the strong basal tine situated very close to the burr and the distal massive fork with posterior insertion of the second crown tine as in *D. eurygonos*. Therefore, the middle tine is missing in the specimen from Capena and the antlers represent the simplified three-pointed type of antler construction. Unlike *D. eurygonos*, the missing middle tine in *D. vallonnetensis* is a constant characteristic, not the early ontogenetic stage of antler development (Croitor 2006a). The fallow deer with such a simplified antler shape are known also from Untermassfeld, Germany (Kahlke 1997, 2001), and Etulia, Moldova (Aleksieva 1977: Tab. XIX). Aleksieva (1977) reported the antlers with skull fragments from Etulia as *Cervus (Rusa) moldavicus*, however, the short and robust pedicles, convex parietal bones, and the three-pointed antlers with the low insertion of first tine and the posterior insertion of third tine on beam are the diagnostic characters of *D. vallonnetensis*.

A somewhat smaller form of *D. vallonnetensis* comes from the final Villafranchian/Epivillafranchian of Pirro Nord (Italy). The material from Pirro Nord is also represented by perfectly preserved articulated skeletons and a complete antlered skull (Fig. 47). The cranial material from Pirro Nord provides several characters that confirm the very close relationship between the Villafranchian fallow deer and *D. dama*: the large and inflated bullae tympani, the flexed neurocranium, the

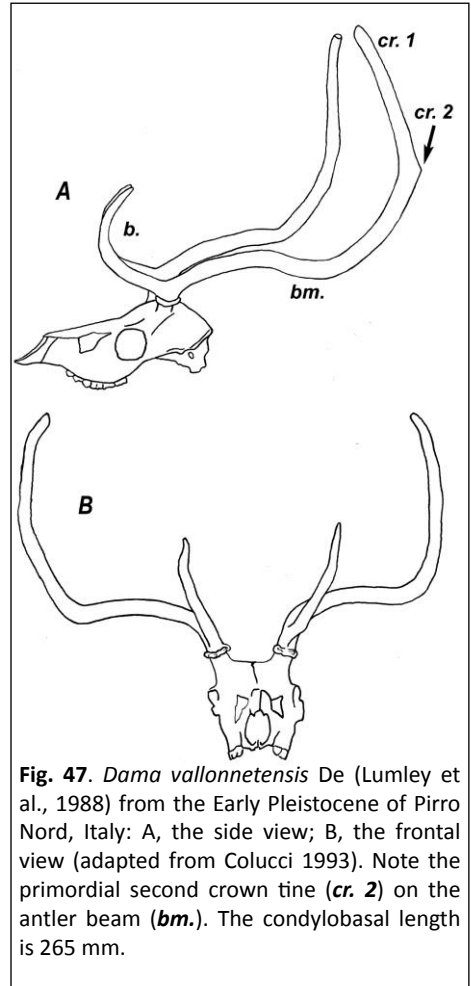


Fig. 47. *Dama vallonnetensis* De (Lumley et al., 1988) from the Early Pleistocene of Pirro Nord, Italy: A, the side view; B, the frontal view (adapted from Colucci 1993). Note the primordial second crown tine (cr. 2) on the antler beam (bm.). The condylobasal length is 265 mm.

broad contact of ethmoidal openings with nasale, and the missing upper canines. The fallow deer from Pirro Nord is characterized by the advanced molarization of P_4 and the relatively short premolar series (premolar/molar ratio varies between 55.3 % and 57.7 %; $n=3$). Unlike *D. dama*, the fallow deer from Pirro Nord is characterized by the short nasal bones, which are not extended behind the line connecting the anterior edges of orbits, the longer contact between the nasal and premaxillary bones, and the very broad and massive praemaxillary bones, which represent an adaptation to arid environmental conditions. The antlers of the fallow deer from Pirro Nord are characterized by an obtuse first ramification situated very close to the burr, vestigial posterior crown tine represented only by a little knob, and missing middle tine (Croitor 2014). The described individual of fallow deer from Pirro Nord is a young adult male, which is very close to *Dama vallonnetensis* (De Lumley et al. 1988) from Capena and Vallonnet.

DAMA CLACTONIANA FALCONER, 1868

This is the largest species of the genus (ca. 140 kg) from the Middle Pleistocene of Western Europe and the first fallow deer species palmated antlers. The antlers of *Dama clactoniana* are distinguished by the presence of multiple crown tines inserted on the anterior and the posterior sides of the palmation axe, unlike modern *D. dama* (Leonardi & Petronio 1976). This deer is characterized by a relatively longer face, however, the face lengthening is different from that of *C. elaphus*: the anterior edge of orbits in *D. clactoniana* is situated above M^2 , as I could see on the specimen "Riano 6" (MPS), indicating that the orbitofrontal part of the skull is not elongated. The facial morphology of partially preserved skull from Swanscomb (Sw-71, NHML) is similar to the fallow deer from Pirro Nord: the nasal bones hardly reach the anterior orbital line, while the articulation between nasal and premaxillary bones is much longer than in *D. dama*.

Another Middle Pleistocene species of fallow deer, *Dama roberti*, was recently described by Breda & Lister (2013) from Pakefield (England) and Soleilhac (France). The antlers are characterised by a typical for *Dama* obtuse basal ramification and a strong curved basal tine. The antler beam is straight, with a narrow flattened expansion in its distal part. Breda & Lister (2013) suggest that the specimen from Pakefield is an adult individual; however its vertically set pedicles (a typical character of *Dama*) are relatively too long indicating the young age of the individual. The articulations between cranial bones (Breda & Lister 2013: 159, fig. 3) are not obliterated, confirming the young individual age. Therefore, there is a high probability, that the unusually simple antlers from Pakefield and Soleilhac represent just an early ontogenetic stage of development. This point of view may be confirmed by the young specimen No. 19 B.M. of *Dama clactoniana* from Swanscomb (Leonardi & Petronio 1976: 22, fig. 28), which is also characterised by presence of the only one basal tine and the distal narrow blade-like extension. Earlier, we reported the antler of fallow deer from Soleilhac as a juvenile specimen of *Dama clactoniana* (Croitor et al. 2006) and we do not see convincing arguments that may change our opinion.

DAMA DAMA (LINNAEUS, 1758)

The oldest fallow deer of modern type was reported by Di Stefano & Petronio (1997) from the middle Aurelian mammal age (late Middle Pleistocene) as a new chronosubspecies *D. dama tiberina*. The new subspecies is distinguished from *D. clactoniana* by its smaller body size and less “hypermorphic” antlers that never evolved anterior crown tines. Unlike *D. dama dama*, *D. dama tiberina* is characterized by narrowed palmation and fewer crown tines on the posterior side of the palmation (Di Stefano & Petronio 1997). Abbazzi et al. (2001) suggested a close relationship between *D. dama tiberina* and *Megaloceros calabriae* Bonfiglio, 1978 from Bovetto, Southern Calabria and defined the deer from Bovetto as *D. dama cf. tiberina*. *Megaloceros calabriae* has a priority over *D. dama tiberina* and if the synonymy of these subspecies named will be proved, the oldest subspecies of the modern fallow deer should be called *D. dama calabriae* (Bonfiglio, 1978). Otherwise, the name *D. dama calabriae* will remain restricted to the fallow deer from Bovetto.

D. dama geiselana Pfeiffer, 1998 is a large form of fallow deer from Northwestern Europe comparable in size to *D. clactoniana*. The antlers are terminated with a strong palmation that forms in its lower part a more or less detached posterior tine. The basal tine is strong and cylinder-shaped. Some variants of antler morphology with the flattened in its proximal part beam and the supplementary small prongs between the basal and middle tines remind *Dama mesopotamica*. P_4 is variable and in some cases is not fully molarized. *D. dama geiselana* is distinguished from *D. clactoniana* by the shape of palmation and absence of the anterior crown tines (Pfeiffer 1998).

DAMA CARBURANGELENSIS (DE GREGORIO, 1925)

This small-sized (ca. 62 kg) endemic deer from the post-Tyrrhenian age of Sicily (late Middle Pleistocene – Late Pleistocene) was regarded as a dwarfed insular giant deer *Praemegaceros (Notomegaceros) carburangelensis* (Gliozzi & Malatesta 1982). Abbazzi et al. (2001) recognized the close affinity of the Sicilian endemic deer with modern fallow deer. Thus, *Notomegaceros* Gliozzi & Malatesta, 1982 becomes a junior synonym of *Dama*. The cranial morphology reported by Gliozzi & Malatesta (1982) is typical for *Dama*. Antlers of *Dama carburangelensis* possess a strong basal tine, a middle tine, and a small, but clearly developed distal palmation with three posterior crown tines. There is an accessory tine situated above the middle one on the posterolateral side of the beam. It could be just an accidental accessory prong, or an analogue of the posterior tine seen in the cervids adapted to open landscapes (*Megaloceros giganteus*, *Praemegaceros verticornis*, *Rangifer tarandus*, etc.). If this is the case, we are dealing with an interesting convergent instance of development of a posterior tine in *Dama*. The species maintains the typical for cervids brachiodont type of dentition. The mean value of premolar/molar ratio (60.4%) reported by Gliozzi & Malatesta (1982) indicates a comparatively longer premolar series than in the continental fallow deer. In this respect, *D. carburangelensis* reminds another Mediterranean insular deer, *Praemegaceros cazioti*, that evolved relatively long cheek tooth row due to the elongation of the premolar series.

CERVINAE INCERTAE SEDIS***“CERVUS” AUSTRALIS* DE SERRES, 1838**

The systematic position of this *Capreolus*-sized plesiometacarpal deer is not resolved yet. The species is based on a small shed antler with a very high position of a single bifurcation from the Early Pliocene of Montpellier, France (de Serres 1838). The additional material from the type locality is unknown. Depéret (1890) assumed that *Cervus* (*Capreolus*) *ruscinensis* based on a fine antlered skull of with spike-like antlers could represent a young individual of *“Cervus” australis* (regarded by Depéret as *Capreolus australis*). Despite of the assumed young individual age of the type specimen of *Cervus* (*Capreolus*) *ruscinensis*, it is characterized by very short and quite divergent pedicles. Korotkevich (1970) and Vislobokova (1990) included *“Cervus” australis* in the genus *Paracervulus*. It is necessary no mention that the antler with pedicle from Kuchurgan described by Korotkevich (1970) as *“Paracervulus australis”* is characterized by a relatively long pedicle. Teilhard de Chardin & Trassaert (1937) created the genus *Paracervulus* for quite large cervids with simple antlers characterized by a high-situated bifurcation. Possibly, some of specimens described by Teilhard de Chardin & Trassaert (1937: fig. 4, *Paracervulus bidens*) belong to *Procapreolus*. Simpson (1945) regarded *Paracervulus* as a junior synonym of *Metacervulus* Teilhard de Chardin & Trassaert, 1937. Asian *Metacervulus* is distinguished from *“Cervus” australis* and *“Cervus” ruscinensis* by its flattened antlers. Therefore, the systematical position of *“Cervus” australis* and *“Cervus” ruscinensis* remains uncertain.

CERVIDAE INCERTAE SEDIS

Genus *Croizetoceros* Heintz 1970*CROIZETOCEROS RAMOSUS* (CROIZET & JOBERT, 1828)

This is a rather small-sized plesiometacarpal deer from Pliocene and Early Pleistocene (MN16-18) with large complicated antlers and advanced morphology of dentition (Heintz 1970). The estimated body mass is about 50-55 kg. The antler shape of *C. ramosus* is peculiar and does not show a clear affinity with any known group of cervids. The basal tine is situated high above the burr and then is followed by a series of crown tines inserted on the anterior side of the beam,

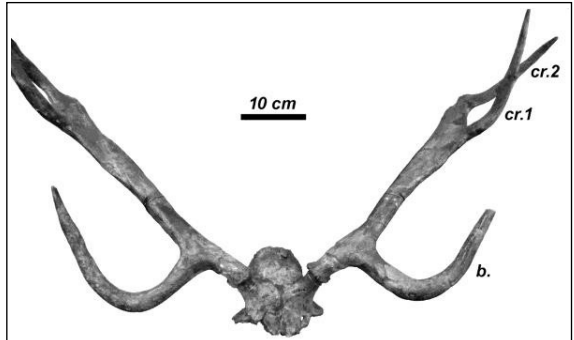


Fig. 48. The antlered skull Nr. 1923-4 (MNHN) of *Croizetoceros ramosus* (Croizet & Jobert, 1828) from Sênèze.

with more or less equal distance between them; a fully grown antler may evolve 6-8 tines (Heintz 1970). The morphology of the cheek teeth shows the unusual for Pliocene Cervinae combination of characters: P_4 is always molarized, the *Palaeomeryx* fold can be vestigial or missing, and the small protoconal fold and hypoconal enamel spur are present in upper molars. The cranial remains of *C. ramosus* are rather scanty and do not provide systematically important characters. The antlered skullcap 1923-4 from Sênèze (MNHN) is one of the most complete specimen (Fig. 48). The frontal bones are flattened, the forehead behind orbits is sharply narrowed (the breadth at posterior edges of orbits is 118.5 mm; the frontal breadth is 85.3 mm; the breadth behind pedicles is 71.6 mm); the pedicles are rather short (their length does not exceed transversal diameter), divergent, some-what inclined caudally; the parietal bones are flat; the braincase seems to be relatively long. According to Heintz (1970), the preorbital pits are large and deep, the ethmoidal openings are large. Heintz (1970) also quotes the statement of J. Viret on presence of upper canines. The relative length of the lower premolars is as in *Pliocervus* (66%). The doubtless evidence of the presence of *C. ramosus* in Central and Eastern Europe is missing with the exception of some scanty Early Villafranchian remains from Poland and Slovakia (Czyżewska 1972; Stefaniak 1995, 2015; Sabol 2003). *C. ramosus* was abundant in the Villafranchian of Western and Mediterranean Europe (Heintz 1970; Kostopoulos & Athanassiou 2005) and got extinct soon after the *Pachycrocuta*/"wolf" event. It seems that *C. ramosus* was an ecological counterpart of *Procapreolus moldavicus*, which, in its turn, is not known in Western Europe, but is common in Central and South-Eastern Europe. There are no remains of *Croizetoceros* or a similar cervid found in Asia, a fact that allows us to assume that *Croizetoceros* is an endemic European genus. Dong (1996) described *Croizetoceros proramosus* from the Early Pliocene of France. The species is based on

dental remains only and we know nothing about its antlers and other part of skeleton. This species is already characterized by the advanced molarization that distinguish it from the deer of the subfamily Cervinae of that epoch.

Mennecart et al. (2017) revealed the close relationship between *Procapreolus pyrenaicus* (*Croizetoceros pyrenaicus* fide Mennecart et al. 2017) and *Croizetoceros ramosus*. According to the results of bony labyrinth analysis, *Croizetoceros* is placed in a sister position to the crown Capreolinae (*ibidem*). Therefore, *Croizetoceros* is suggested as a curious case of the plesiometa Carpality that evolved independently from Cervinae. However, a caution is needed in this case, since the size of smallest *Croizetoceros ramosus* overlap with largest *Procapreolus cusanus* (Heintz 1970). Therefore, for the moment, better to keep *Croizetoceros* as a genus *incertae sedis* until the confirmation of the results of Mennecart et al. (2017) will be done.

EVOLUTION AND PHYLOGENY

The dichotomy of the family Cervidae described by Brooke (1878), who divided all cervids into the informal groups of Plesiometacarpalia and Telemetacarpalia, is confirmed by modern molecular phylogenetic studies (Pitra et al. 2004; Gilbert et al. 2006). The mitochondrial and nuclear DNA analysis supports the monophyletic character of the subfamily Cervinae (plesiometacarpal “Old World deer”) in its traditional understanding (Pitra et al. 2004). It was also demonstrated that the primitive tropical plesiometacarpal cervids with simple two-pointed antlers, which traditionally were included in the “primitive” subfamily Muntiacinae, is a sister phylogenetic group of cervines and the cervine-muntiacine branch is opposed to the “New World deer” and Eurasian telemetacarpal *Capreolus*, *Alces* and *Hydropotes* (Pitra et al. 2004; Gilbert et al. 2006). Therefore, at least among modern cervids, the plesiometacarpal type of forelimbs occurred only once. The evolutionary radiation of Cervines is zoogeographically compact, centered in the eastern part of the Oriental zoogeographic province, and remains generally intact until the present days (Geist 1988). The taxonomy of the subfamily Cervinae is still poorly developed at the tribal level and therefore I shall confine myself to simply indicating the phylogenetic lineages and their presumed place within the phylogenetic tree of Cervinae.

According to Mennecart et al. (2017), the Middle-Late Miocene *Eurpox furcatus* and the Early Pliocene “*Cervus*” *rusciniensis* represent the early phylogenetic branches of Cervinae that preceded the evolutionary radiation of the modern plesiometacarpal deer. Both *E. furcatus* and “*C.*” *rusciniensis* attained the body size of the modern roe deer and maintained the simple bifurcated antlers. The small-sized *Euprox pidoplitschkoi* from the Early Pliocene of Eastern Europe and the Early Villafranchian of the Italian Peninsula is a probable descent of *E. furcatus*. Unlike *E. furcatus*, *E. pidoplitschkoi* is characterized by the relatively shorter pedicles and the smaller body size as in modern *Muntiacus*. The difference in relative length of pedicles between *E. furcatus* and *E. pidoplitschkoi* corresponds to the difference in pedicle length between modern *M. muntjac* and *M. reevesi*.

The first cervines with large complicated antlers from the Early Pliocene (MN14-15) of the European Subcontinent (*Metacervocerus* and *Praeelaphus*) have a sister relationship to the modern genus *Axis*. *Praeelaphus* is more advanced in its large four-tined antlers with complicate morphology, however the dental and cranial morphology generally remains primitive as in *Axis* and *Metacervocerus* (Croitor 2017). *Metacervocerus* and *Praeelaphus* did not give an important evolutionary radiation in the European Subcontinent and got extinct with the end-Villafranchian faunal turnover.

Arvernoceros from Late Pliocene of Europe shows a remarkable bauplan of antlers shared with modern *Rucervus* and *Sinomegaceros* (van der Made & Tong 2008; Croitor 2009, 2016). Unlike *Rucervus*, *Arvernoceros* and *Sinomegaceros* evolved a small distal palmation. The evolutionary relationships between *Rucervus*, *Arvernoceros*, and *Sinomegaceros* are not clear yet and require new data on cranial morphology

that are needed to reveal the taxonomic status and more exact systematic position of *Arvernoceros* and *Sinomegaceros*. This phylogenetic branch is represented in the Late Pliocene and Early Pleistocene of western Eurasia by several forms, which are still poorly known and misunderstood and often are reported as *Eucladoceros*, *Praemegaceros* or *Megaloceros*. All *Rucervus*-like deer from the Western Palearctic are included here in the genus *Arvernoceros* until the taxonomical and systematical issues will be resolved. Apparently, the diversity of *Rucervus*-like species and forms does not represent a local evolutionary radiation and this is one of the reasons of the caution. The *Rucervus*-like cervids dispersed into the Western Palearctic in different faunal turnover contexts and from different paleobiogeographic areas, as, for instance, *Arvernoceros giulii*, a large cursorial form evolved in the temperate latitudes of Asia, or *Arvernoceros verestchagini*, which shows affinity with “*Cervus*” *colberti* from Sivalik Hills of Southern Asia. The lineage of *Rucervus*/*Arvernoceros* survived in the Iberian glacial refugium as the endemic specialized form *Haploidoceros mediterraneus* until Late Pleistocene.

The tribe Megalocerotini Brookes, 1828 *sensu lato* (= Megacerini Viret, 1961 *vide* Vislobokova 1990, 2009, 2012, 2013) in its traditional understanding is a polyphyletic group. The analysis of cytochrome *b* sequence of the extinct giant deer *Megaloceros giganteus* has revealed its close phylogenetic relationship with *Dama dama* and *Dama mesopotamica* (Lister et al. 2005; Hughes et al. 2006). The earliest remains of *Megaloceros giganteus* are dated back to ca. 400 kyr BP (Lister 1994; Lister et al. 2005), however, the estimated divergence of *Dama* and *Megaloceros* could have occurred much earlier (Hughes et al. 2006), well before the forerunner of *Dama* dispersed in Western Eurasia. The tribe Megalocerotini Brookes, 1828 *sensu stricto* with the genera *Megaloceros*, *Megacerooides*, and *Dama* represent a genuine phylogenetic branch, however, we need a more scrupulous comparative morphological study in order to establish an adequate taxonomical definition of the tribe if there is a need to keep this taxon. The present state of knowledge does not provide a satisfactory diagnosis for this restricted group of genera containing extremely specialized forms.

The cervid forms grouped under the term “giant deer” or “large-sized deer” actually represent several lineages that evolved similar convergent adaptations in the similar conditions (open landscape of temperate latitudes). The large body size, the large and complicated palmated antlers that have a function of visual intraspecific communication, and the posterior tine should be mentioned as the specific “giant deer” morpho-functional adaptations that appears independently in several species adapted to open-landscape (*Rangifer tarandus*, *Megaloceros giganteus*, *Dama dama geiselana*, *Praemegaceros verticornis*, *Sinomegaceros yabei*). The mandibular and cranial pachyostosis reported as an important diagnostic character of megacerines (Vislobokova 1990; 2009; 2012; 2013) actually is a secondary metabolic response to exogenic factors, primarily the marked seasonality (Lister 1994; Croitor 2006b, 2016). It is worth noting that all known pachyostotic cervids belong to the subfamily Cervinae and evolved and lived in the most peripheral and extreme parts of the distribution area of this subfamily. This is the case of the periglacial giant *M. giganteus*. *Sinomegaceros*

pachyosteus is another pachyostotic cervine species that may have been affected by the repeatedly advancing arid zones of Central Asia. Similarly, *Megaceroides algericus* evolved in the Atlas refugium of the North African arid zone. Van der Made & Tong (2008) found signs of mandibular pachyostosis in a wide variety of cervids and assumed that this specific character converged several times among cervids and denied its evolutionary significance for the group of giant deer. Therefore, the sporadic occurrence of mandibular pachyostosis in various cervid lineages cannot be used as a meaningful systematic character at the tribe level.

The genus *Dama* is peculiar in its zoogeographic remoteness from the radiation centre of the Cervinae: this highly evolved lineage appears in the Early Pleistocene of Western Palearctic (Italy, Moldova) and does not show any morphological characteristics that demonstrate clear relationship with cervines from the Oriental zoogeographic province. The divergence of *Dama* from *Cervus* and allied cervines from South-Eastern Asia took place during Early Pliocene (Pitra et al. 2004), or around 3.0 Ma (Gilbert et al. 2006).

Megaloceros is characterized by more primitive cranial morphology if compared to the fallow deer. The plesiomorphic morphological condition is expressed in the less flexed braincase and the inclined position of pedicles. *Megaloceros giganteus* was characterized by vast boreal distribution ranging from Ireland to Central Siberia (Lister et al. 2005). The exact area of giant deer origin is unknown. *Megaloceros giganteus antecessens* is the earliest form of giant deer in Europe that shows the adaptations to wooded ecosystem and, most probably, is a side specialized form of the giant deer lineage. The apparent “*Sinomegaceros*”-like antler shape of *M. giganteus antecessens* resulted from the significant shortening of antlers that caused the coalescence of the middle and posterior tines with the distal palmation. *Megaloceros mugharensis* from Near East is another Middle Pleistocene specialized form characterized by the reduced body size and shortened limb bones characteristic of the endemic Mediterranean cervids (for example, *Cervus elaphus rianensis* from Italy). *Megaceroides algericus* from Late Pleistocene and Holocene of North Africa probably is a descent of *M. mugharensis* (Croitor 2016). Therefore, *Megaloceros* represents one of the few exceptional cases of colonization of North Africa by cervids, possibly, due to its physiological capacity to tolerate the brief seasonal shortage of food supply.

The suggested by Radulesco & Samson (1967) and Azzaroli & Mazza (1992b, 1993) phylogenetic relationship between *Eucladoceros* and *Praemegaceros obscurus* is apparently correct, however, the character of this phylogenetic relationship is more complicated. The demonstrated by Mennecart et al (2017) similarity in bony labyrinth morphology of *Eucladoceros ctenoides* and *Cervus elaphus* is interesting, since one of the species of the *Cervus* phylogenetical stock, the Thorold’s deer *Przewalskium albirostris*, is characterized by a comb-like antler bauplan as *Eucladoceros*.

One can assume that *Praemegaceros obscurus* is a south Asian large-sized form that shows a great affinity in antler morphology with modern *Panolia eldi*, another species from the *Cervus* phylogenetic stock. It is necessary to mention that according to some

authors, *Przewalskium albirostris* and *Panolia eldi* should be included in the genus *Cervus* (Pitra et al. 2004). *Praemegaceros pliotarandoides* and *P. verticornis*, apparently, are closely related to *P. obscurus*, however, morphologically are more distant from *Panolia eldi*.

The phylogenetic relationships of the lineage *Praemegaceros solilhacus* - *Praemegaceros cazioti* cannot be demonstrated yet, despite of the available well-preserved skulls of *P. cazioti*. Generally, the cranial shape of *P. cazioti*, despite of its pronounced adaptation to grazing, is still very close to the generalized primitive morphology seen in *Eucladoceros* or *Axis*.

The early radiation within the genus *Cervus sensu stricto* and the consequent early dispersals of this genus in the Western Palearctic is confirmed by the occurrence of *Cervus nestii* in the Early Pleistocene of Olivola, Upper Valdarno (Italy), and Dmanisi (Georgia). This small cervid is already characterized by the typical for modern red deer cranial morphology, including the elongated splanchnocranium (especially its orbitofrontal portion) combined with the “*Muntiacus*”-like narrow triangular basioccipitale. The frontal orientation of the distal antler fork is another specific character shared by *Cervus nestii* and the primitive subspecies of red deer, like *C. elaphus acoronatus* and *C. elaphus bactrianus*. The Barbary stag *Cervus elaphus barbarus* from North Africa could be related to the evolutionary stage of the red deer lineage represented by *C. nestii*. According to Geist (1998) and Pitra et al. (2004), the Barbary stag is a pedomorphic form with the secondary simplified antlers that lost their bez tine. The white spots on the back of the mature Barbary stag is another primitive characteristic reported only for this form of red deer (Geist 1998). The taxonomical and evolutionary status of Barbary stag is still discussed. Pitra et al. (2004) and Groves & Grubb (2011) support the full species status for the North African red deer. The analysis of mitochondrial DNA resulted the particularly long time of divergence (2.2 Ma) between *C. elaphus barbarus* and Eurasian red deer (Ludt et al. 2004). According to Ludt et al. (2004), the African and Sardinian red deer could be exposed to the recent gene drift that possibly explain their high differentiation from the other subgroups.

The red deer *Cervus elaphus* is represented by several subspecies and forms in the Middle and Late Pleistocene of Western Eurasia. This diversity of forms most probably resulted from the combination of several dispersal events from the east and local evolutionary processes in the western (the Iberian Peninsula) and eastern (the Italian Peninsula, Balkans, and Anatolia) glacial refugia. The Italian Peninsula as a paleozoogeographic case is interesting, since during the glacial periods it had a broader connection with the Balkan Peninsula and acted as a part of Balkan-Italian glacial refugium. The geographic isolation of the Italian Peninsula during the interglacial periods caused the partial isolation of local red deer populations that created the conditions for local evolution of such forms as *C. elaphus rianensis*, *C. elaphus aretinus*, as well as the endemic form of wapiti with palmated antlers *C. canadensis palmidactyloceros*.

The rich diversity of Cervinae in Western Palearctic resulted from the more or less episodic dispersal events, while the importance of local evolutionary radiation remained

insignificant. The genus *Dama* with up to seven species and, possibly, the genus *Praemegaceros* with up to nine species (however, the monophyly of *Praemegaceros* in its current understanding is not demonstrated yet) represent the exceptional cases of local evolutionary radiation that includes also the instances of the speciation in the insular isolation (*Dama carburangelensis*, *Praemegaceros cazioti*, *Praemegaceros dawkinsi*).

The available paleontological information on evolutionary radiation of the telemetacarpal deer is quite incomplete. It seems that the Late Miocene radiation of Capreolinae was initially represented by the range of forms with various degree of evolutionary specialization and included the whole spectrum of ecological and evolutionary forms, such as *Cervavitus* with large palmated antlers, the *Muntiacus*-like *Procapreolus* from Eastern Europe, *Pliocervus* from Western Europe and *Pavlodaria* from Kazakhstan with large upper canines and four-tined antlers. The holometacarpal limbs are assumed at least for *Cervavitus*, however, the holometaparpality of Late Miocene cervids from Eastern Europe is not demonstrated yet (Azanza et al. 2013). I do not exclude that some of cervid remains reported as *Cervavitus* and *Procapreolus* are still poorly understood and misinterpreted.

The *Palaeomeryx* fold is regarded here as an important diagnostic character for primitive Capreolinae: it is recorded in all archaic Old World genera of Capreolinae (*Pliocervus*, *Pavlodaria*, *Procapreolus*, *Cervavitus*, *Capreolus*, *Alces*) and in some lineages (the genus *Alces*) this morphological character is maintained until the Middle Pleistocene. Unlike Cervinae, the antler construction in Capreolinae is rather uniform. The basic tree-pointed “roe deer type” antler bauplan is recognizable in all modern and fossil Capreolinae with large complicate antlers, even in such specialized genus as *Alces*. *Pliocervus* and *Pavlodaria* show a different antler bauplan characterized by four-pointed antlers: two proximal tines are situated on the anterior side of the beam, which is terminated by the distal fork (Croitor, work in progress).

The phylogenetical clade of modern Eurasian Capreolinae is significantly depleted, since many of evolutionary branches gone extinct (Geist 1998). This is one of the reasons why the few survived Eurasian genera of Capreolinae are so contrastingly different one from another. This can be explained by the fact that the adaptive radiation of Capreolinae took place in the temperate latitudes of Eurasia, which were stronger affected by climate changes. Unlike coeval Cervids from the Oriental adaptive radiation, the Late Miocene “crown cervids” from Eastern Europe share the quite uniform morphology of dentition, which shows a different evolutionary way: lower molars in all European and North Asian genera (*Procapreolus*, *Cervavitus*, *Pliocervus*, *Pavlodaria*) are reinforced with the *Palaeomeryx* fold, lower fourth premolar (P_4) has a trend toward the early advanced molarization (*Procapreolus moldavicus*, *Cervavitus variabilis*, *Pavlodaria orlovi*) in the combination with the relatively long premolar series.

One can assume that *Procapreolus* characterized by the muntjac-like traits of cranial morphology (large preorbital pits, long sloped backward pedicles, large upper canines) represents an early off-shoot of the Capreolinae phylogenetic tree. This presumption is

based on the detached phylogenetic position of *Procapreolus pyrenaicus* with respect to the rest of Capreolinae revealed by Mennecart et al. (2017). This viewpoint is different from the earlier hypothesized phylogenetic model that regards *Procapreolus* as a direct forerunner of *Capreolus* (Korotkevich 1970; Vislobokova & Kalmykov 1994; Valli 2010).

The phylogenetic position of *Capreolus* is linked to the group of telemetacarpal deer characterized by the incomplete division of the nasal cavity by the vertical plate of vomer that includes also *Alces* and *Hydropotes*. The monophyly of this group is supported by the genetic analysis (Pitra et al. 2004) and the analysis of the bony labyrinth morphology (Mennecart et al. 2017).

The origin of *Alces* could be related to a cervid similar to *Cervavitus variabilis*, which is characterized by short and comparatively stronger divergent pedicles and large antlers that have a tendency to evolve palmations. *Cervavitus variabilis* shares with *Alces* (including *Alces gallicus*) general plan of antler construction, the relatively long lower premolar series, the advanced molarization of P₄, and the *Palaeomeryx* fold in lower molars. The genus *Alces* perfectly fits to the extrapolation of the evolutionary specialization seen in *Cervavitus variabilis*.

The elk species described from Pleistocene of Western Europe, most probably, do not belong to a successive phyletic lineage, but represent the side specialized branches. This is the case of *Alces gallicus*, the earliest known in Europe species of elks, which is already characterized by an extreme specialization of antler morphology with a very large antler span caused by the elongation of the basal segment of antler. The dry temperate planes of Asia are the area of origin and initial evolution of *A. gallicus*. This species together with *Cervalces scotti* represents the first successful dispersal of elks in the temperate latitudes of Eurasia and North America.

Pavlodaria and *Pliocervus* represent another group of Eurasian telemetacarpal deer characterized by the complete division of the nasal cavity by the vertical plate of vomer and more complicate four-pointed antler bauplan. Apparently, this group of telemetacarpal deer also includes *Rangifer*, as it was already suggested by Korotkevich (1970). This assumption is supported by the position of parallel and deflected backward pedicles in the primitive form of *Rangifer sp.* from the Early Pleistocene of Isakovka-4 (Russia) (Bondarev et al. 2017) shared with *Pavlodaria* and *Pliocervus*. Possibly, the indicated phylogenetic groups of the Old World telemetacarpal deer could be regarded as tribes, however, more data are needed to demonstrate the taxonomical significance of the above mentioned phylogenetic groups.

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Notes