Deer from Late Miocene to Pleistocene of Western Palearctic: matching fossil record and molecular phylogeny data

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Abstract

This article proposes a brief overview of opinions on cervid systematics and phylogeny, as well as some unresolved taxonomical issues, morphology and systematics of the most important or little known mainland cervid genera and species from Late Miocene and Plio-Pleistocene of Western Eurasia and from Late Pleistocene and Holocene of North Africa. The Late Miocene genera *Cervavitus* and *Pliocervus* from Western Eurasia are included in the subfamily Capreolinae. A cervid close to *Cervavitus* could be a direct forerunner of the modern genus *Alces*. The matching of results of molecular phylogeny and data from cervid paleontological record revealed the paleozoogeographical context of origin of modern cervid subfamilies. Subfamilies Capreolinae and Cervinae are regarded as two Late Miocene adaptive radiations within the Palearctic zoogeographic province and Eastern part of Oriental province respectively. The modern clade of Eurasian Capreolinae is significantly depleted due to climate shifts that repeatedly changed climate-geographic conditions of Northern Eurasia. The clade of Cervinae that evolved in stable subtropical conditions gave several later radiations (including the latest one with *Cervus*, *Rusa*, *Panolia*, and *Hyelaphus*) and remains generally intact until present days. During Plio-Pleistocene, cervines repeatedly dispersed in Palearctic part of Eurasia, however many of those lineages have become extinct.

Key words: Cervidae, systematics, evolution, molecular phylogeny, paleontological record.

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1. Introduction

Deer represent one of the most successful and rich in species group of large-sized herbivores in modern fauna of Eurasia and Americas. In the geological past, family Cervidae was represented by a significantly broader variety of evolutionary and ecological forms, which exemplify some interesting biogeographic and evolutionary examples of parallelism, the convergence, the broad phylogenetical radiation in a newly colonized mainland, the evolution in conditions of insular isolation, or the evolving of endemic forms in biogeographic refugia (Lydekker 1898; Lister 1987; Vislobokova 1990; Geist 1998; Croitor 2006b; Croitor et al. 2006). However, many of fossil cervid forms are poorly known, imperfectly described, or misunderstood. The situation is complicated by multiple synonymies and lack of methodologically uniform criteria applied in taxonomy and systematics of fossil cervids. Despite the fact that during more than a century of study of cervid systematics a great variety of cervid classification schemes were proposed, a visible progress had not been reached.

The first attempt to build a founded classification of the family Cervidae belongs to Brooke (1878) who described in cervids two types of reduction of the second and fifth metacarpals represented by their proximal (plesiometacarpal condition) or distal (telemetacarpal condition) remnants. According to the reduction type of lateral metacarpals, Brooke (1878) established two cervid groups: group "Plesiometacarpi" that includes the Old World deer with exception of *Capreolus* and *Hydropotes*, and group "Telemetacarpi" that includes mostly the New World deer (with exception of *Cervus elaphus canadensis*), the Old World genera *Capreolus* and *Hydropotes*, as well as the circumpolar and circumboreal genera *Rangifer* and *Alces*. Among "Plesiometacarpi", 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 telemetacarpal morphological condition and the complete dividing of nasal cavities by vertical plate of vomer in combination with some other morphological characters, there-

fore 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* (but since it is not present in primitive deer like *Procervulus*, *Heteroprox*, *Dicrocerus*, or *Euprox* it seems to be a derived condition for Rangiferini; pers. comm. Beatriz Azanza July 2014). 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 Goldfuss, 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: Cervinae with all modern genera of plesiometacarpal and telemetacarpal deer, as well as extinct genera *Dremotherium*, *Dicrocerus*, and *Anoglochis*[1], and Moschinae 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. Azzaroli (1953) grouped the living deer into seven subfamilies: Cervinae, Muntiacinae, Capreolinae, Odocoileinae, Rangiferinae, Alcinae, and Hydropotinae.

Simpson (1945) proposed the first important systematical generalization of cervids. Simpson (1945) 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 Carette, 1922 (= Capreolinae Brookes, 1828, = Odocoileinae Pocock, 1923); and Hydropotinae Trouessard, 1898. According to Flerov (1952), Late Miocene *Cervavitus* represents a transitional link between muntjac-like *Dicrocerus* and modern *Cervus* and other closely related Cervinae forms, while the rather arbitrary group of "American deer" resulted from the local evolutionary process from Miocene *Blastomeryx*. Flerov (1952) proposed also hypothesized phylogenetic relationships of modern cervid species with fossil forms.

The difficulty in finding the systematical position of fossil deer forms among the modern cervids pushed researchers to create separate taxonomic units for their fossil species. In 1913, Khomenko established the subfamily Pliocervinae in order to designate the transitional evolutionary stage between primitive muntiacines and 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 matheronis* 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 the Article 29 of the ICZN. In 1974, Symeonidis proposed the subfamily Pliocervinae, which can be taken to be based on *Pliocervus* Hilzheimer, 1922 (founded on *C. matheronis*), 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, is another taxonomic unit created as a receptacle for Old World fossil cervids with obscure phylogenetic relationships. This taxonomic group was accepted by some of researchers (Czyzewska 1968; Lister 1987; Vislobokova 1990, 2009; di Stefano & Petronio 2002). Vislobokova (1990, 2009, 2012, 2013) regarded the giant deer as a well-separated phylogenetic group of cervines and included in the tribe Megacerini up to 11 genera from Eurasia and Mediterranean islands with 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.

Czyzewska (1968) followed the cervid classification proposed by Flerov (1952) and proposed to distinguish the following tribes within the subfamily Cervinae Baird, 1857: Pliocervini Khomenko, 1913 with the genus *Cervavitus* Khomenko, while *Pliocervus*

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[1]*Anoglochis* Croizet et Jobert is a polyphyletic poorly defined genus, which was regarded by some authors as a synonym of *Capreolus* (see, for instance, de Serres 1830: p. 125) or *Eucladoceros* (Lydekker 1898: p. 238).

Hilzheimer, 1922 is regarded as *incertae sedis* (sic!); Capreolini Simpson, 1945, Cervini Weber, 1928; Alcini Simpson, 1945; and Megacerini Viret, 1961. According to Czyzewska (1968), the genus *Euprox* (subfamily Cervulinae = Muntiacinae) is ancestral for two sister lineages: Capreolini and Pliocervini+Cervini. Czyzewska (1968) regarded Asian Pliocervini as the probable ancestors of *Axis* and *Cervus*. Recently, Petronio et al. (2007) attributed the authorship of the tribe Pliocervini to Czyzewska 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) proposed to include muntjaks in their own family Muntiacidae. Grubb (2000) carried out a detailed account on Cervid taxonomy and proposed some emendations for the classification of fossil and modern deer. According to 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 muntjaks from South-Eastern Asia and the extinct Chinese genus *Eostyloceros*. Grubb's (2000) most interesting systematical solution concerns "primitive" muntjac-like cervids, which were included in two different subfamilies: Lagomerycinae and Cervinae.

The karyotype, morphological, and biochemical data involved by Bouvrain et al. (1989) in the systematical study of modern Cervidae 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.

With some modifications, Vislobokova (1990) accepted Simpson's (1945) classification 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 Early and Middle Miocene. According to Vislobokova (1990),

the modern genus *Muntiacus*, together with extinct *Eostyloceros*, *Paracervulus* and *Metacervulus*, take their origin from Early and Middle Miocene Eurasian *Euprox*. The forerunner of Cervinae is also sought among Middle Miocene Muntiacinae (genus *Dicrocerus*). Vislobokova (1990) accepted the tribe Pliocervini Khomenko, 1913 within the subfamily Cervinae with genera *Cervavitus* Khomenko, 1913 and *Pliocervus* Hilzheimer, 1922, stipulating the uncertain systematic position of *Pliocervus*.

The study of systematics and evolution of the subfamily Cervinae proposed by di Stefano & Petronio (2002) is rather contradictory. As stated di Stefano & Petronio (2002: p. 311), "the family Cervidae Goldfuss, 1820 is commonly divided into three groups, subfamilies Hydropotinae Troussard, 1898, Muntiacinae Pocock, 1923, and Cervinae Goldfuss, 1820", without, however, giving any reference to the source of this "common" division. Di Stefano & Petronio (2002) rejected the taxonomical significance of reduction type of lateral metacarpal bones with a reference to the earlier study of Lister & Chapman (1988), but this reference is not reliable. The study of Lister & Chapman (1988) describes a broad variability of atavistic vestiges of lateral metacarpals caused by genetic bottleneck and inbreeding in British populations of fallow deer, and assumes a possibility of parallel development of plesiometacarpality in Muntiacinae and Cervinae. Di Stefano & Petronio (2002) lumped together all antlered telemetacarpal deer and plesiometacarpal cervids with large complicated antlers. The authors included in the subfamily Cervinae six modern tribes (Neocervini Kalandadze & Rautian, 1992 (actually, the authorship belongs to Carette 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 authors' claim that Flerov (1952) proposed to split the subfamily Cervinae in several tribes is untrue.

The proposed here brief survey of various views on classification, phylogeny and evolution of cervids reveals the imperfect knowledge of fossil record of cervids partly due to missunderstood evolutionary significance of morphological characters of modern cervid species, partly due to incomplete paleontological record, and partly due to superficial, inadequate, or inaccurate description of fossil forms. Eurasian telemetacarpal deer (*Capreolus* and *Hydropotes*) and the circumboreal *Alces* for many decades represented the most difficult systematical problem. Antlerless *Hydropotes* was often opposed to all antlered deer and placed in a separate subfamily Hydropotinae (Flerov, 1952; Azzaroli 1953; Groves & Grubb 1987; Vislobokova 1990; Danilkin 1999; Grubb 2000; di Stefano & Petronio 2002).

The specialized genus *Alces* with Early Pleistocene Eurasian *Libralces gallicus* and Middle Pleistocene *Cervalces latifrons* (*Libralces* and *Cervalces*

also are regarded as synonyms of *Alces*) often are placed in the separate subfamily Alcinae (Azzaroli 1953; Vislobokova 1990; Boeskorov 2001). Flerov (1952) and Sokolov (1959) included *Alces* in the subfamily Cervinae. The difficulty in revealing phylogenetical relationships of phyletical lineage of elks mostly is caused by the extreme morphological specialization of their antlers and skulls that do not permit to reveal any obvious link to other cervid groups. 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 Neogene.

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

Although the systematical position and taxonomical status of the modern Eurasian cervines generally did not provoke controversial opinions, nonetheless, some questions remained unresolved. The relationship between modern Old World muntiacines and cervines requires an additional study. Traditionally, muntjacs and large plesiometacarpal deer with complicate antlers are placed in separate subfamilies or even 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. Among other unsolved systematic problems could be mentioned the phylogenetic relationships among modern cervids, which remained as rather arbitrary interpretations based on a limited set of selected characters: antler and cranial morphology (Vislobokova 1990), antler shape (di Stefano & Petronio 2002), postcranial morphology (Pfeiffer 1999, 2004), or general eco-morphology (Flerov 1952). The boundaries between some cervine genera (especially between *Cervus* and other closely related cervid groups), or between species within some genera (for instance, European red deer and American wapiti) (Geist 1998) also remained unclear.

During the last two decades, the analysis of various DNA sequences made a great advance in the understanding of the phylogeny of modern cervids (Miyamoto et al. 1990; Douzery & Randy 1997; Randi et al. 1998; Pitra et al. 2004; Gilbert et al. 2006; Has-

sanin et al. 2012). According to the molecular phylogeny studies, the divergence between plesiometacarpal and telemetacarpal deer is an important basic event in modern cervid phylogeny that took place in 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 close phylogenetic relationship between the modern *Capreolus* and the antlerless *Hydropotes* is revealed; all Old World telemetacarpal cervids (*Alces*, *Capreolus*, and *Hydropotes*) together with New World 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 originated during the Middle Miocene between 15.6 and 16.8 Ma ago, and is very divergent from New World tribes of Capreolinae (Odocoileini and Rangiferini) (Randi et al. 1998). Hassanin et al. (2012) report a more recent dichotomy of Eurasian (including *Alces*) and American Capreolinae (8.7-9.6 Ma).

The strong support for the close phylogenetic association between Cervinae and Muntiacinae (Miyamoto et al. 1990; Pitra et al. 2004; Gilbert et al. 2006) apparently was less expected since the modern muntjacs together with extinct muntjac-like primitive cervids traditionally were placed in the subfamily Muntiacinae at the base of 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 plesiometacarpalian condition probably evolved once among modern cervids through the reduction of lateral metacarpals, and indicates that modern plesiometacarpal cervids represents a natural group (Randi et al. 1998).

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) reported a phylogenetic split between *Axis axis*, *Rucervus schomburgki*, and *Rucervus duvauceli* on one hand, and the remaining Cervinae on the other at the base of the 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 Early Pliocene (Pitra et al. 2004), or around 3.0 Ma (Gilbert et al. 2006). The results of molecular phylogeny analysis also revealed the importance of hybridization in cervid evolution and origin of modern 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 bizarre species *Elaphurus davidianus*. The genus *Elaphurus* apparently is a result of hybridization ♀*Rucervus eldi* (or a very close form) × ♂ *Cervus canadensis* (Meijaard & Groves 2004; Pitra et al. 2004).

The exciting results of implication of genetic analysis in cervid phylogeny allowed to correct the systematics of modern deer and to rethink the taxonomical significance of such characters, as antler complexity, mane and rump patch development, which appeared to be related rather to climatic-related lifestyle factors (Groves 2005). Groves & Grubb (2011) amended 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. Capreolinae, according to Groves & Grubb (1987), includes the tribe Rangiferini Brookes, 1828 with circumpolar genus *Rangifer* and all American telemetacarpal genera, the tribe Capreolini Brookes, 1828 with genera *Capreolus* and *Hydropotes*, the tribe Alceini Brookes, 1828 with a single genus *Alces*. 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.

However, all previous attempts to match fossil cervid record with new molecular phylogeny data remained contradictory and controversial. The most debatable issues concern the identification of the ancestral form for the modern large antlered cervines. Pitra et al. (2004), following di Stefano & Petronio (2002), regard the Late Miocene holometacarpal *Cervavitus novorossiae* as the most primitive member of the Cervinae. This viewpoint is based on the old repeatedly quoted in Russian literature hypothesis of Khomenko (1913) on the mixture of muntiacine and cervine characters in the cranial morphology of *Cervavitus*. The reconstruction of cervid ancestral morphotype as a large open landscape dweller with a strong sexual dimorphism, three-pointed antlers, and missing upper canines proposed by Gilbert et al. (2006) is more than controversial. According to Gilbert et al. (2006), the large upper canines of *Hydropotes* and modern Muntiacini, represent a secondary evolutionary acquisition. This daring hypothesis conflicts with the paleontological and anatomical data (Croitor & Stefaniak 2009). Firstly, the fossil record gives clear evidences that the 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; Rössner 1995; Geist 1998). The enlarged upper canines

are well developed in the majority of Miocene Cervidae, including the earliest representatives of Cervinae (apparently, "*Cervavitus*" from China) and Capreolinae (*Cervavitus*, *Pliocervus*, and *Procapreolus* from Western Eurasia) (Vislobokova 1990; Gentry et al. 1999). Furthermore, the ancestral morphotype proposed by Gilbert et al. (2006) cannot explain the presence of useless vestiges of preorbital fossae almost in all Cervidae with various ecological adaptations. It may be unnecessary reminder that the preorbital fossae serve the function of chemical communication in forest deer and achieve the strongest development in Muntiacinae, as well as in the most primitive fossil Capreolinae (*Procapreolus*), and primitive fossil and modern Cervinae (*"Cervavitus" from China*, *Hyelaphus*). As Simpson (1945) rightly pointed out, the classification of living cervids is relatively easy to arrange; nonetheless, despite of great abundance of fossil forms, they shed little light on the phylogenetic interrelationships of modern deer. In the pre-sent work, I propose a synopsis of systematical and taxonomical revision of most important, as well as less known fossil (latest Miocene to Pleistocene) cervid species and genera from western Eurasia with an attempt to reveal their possible phylogenetic relationships matching anatomical, eco-morphological and paleobiogeographic data with recent discoveries in the cervid molecular phylogeny.

2. Research methods and material

The proposed study is based on revision of type material of fossil deer from Europe, taxonomical study and systematical revision. The studied fossil material is stored in the following collections: the Museum of Geology and Paleontology of the University of Florence (MGUF); the Natural History Museum of London (NHML); Musée national de Préhistoire, Les Eyzies-de-Tayac (MNP); Musée National d'Histoire Naturelle, Paris (MNHN); Paleontological Museum of the University of Lyon (PMUL); the Institute of Zoology of University of Wroclaw (IZW), Poland; the Paleontological Institute, Moscow (PIN); the National Museum of Natural History, Kiev (MNHK); the Institute of Zoology, Department of Paleozoology, Chisinau, Moldova (IZC); the Natural History Museum of Bucharest "Grigore Antipa"(NHMB); and the Institute of Speleology "Emil Racoviţă" (ISB), Bucharest. The osteological material of modern deer stored in the MGUF, MNHN, NHML, and IZUW is also involved in the study.

The main methodological problem in the present study is the different approach in 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 (Flerov 1952; Sokolov 1959; Danilkin 1999; Meijaard & Grooves 2004; Leslie 2010), while definitions of the majority of fossil deer taxa are based

mostly on antler morphology (Azzaroli 1953; Heintz 1970; Korotkevich 1970; Pfeiffer 1999; di Stefano & Petronio 2002). This methodological discrepancy is caused by the relative rarity of well-preserved skulls in the fossil record and makes the matching of modern and fossil cervid species difficult, if not impossible. Therefore, the brief review of fossil genera from Western Eurasia is supplemented with more detailed description of the best cranial findings, which were available for study.

The measurements are in accordance with the methodology proposed by von den Driesch (1976). The angle between neurocranium and splanchnocranium is measured according to Vislobokova (1990). Terminology used in this paper (Heintz 1970; Lister 1987; Vislobokova 1990) was chosen according to its general applicability and wide usage in the field. More specific and less widely used terminology for dental and antler morphology proposed in some recent publications is avoided here. The body mass estimation used for eco-morphological description of fossil cervid forms is based on craniodental measurements according to the regression equations proposed by Janis (1990). The cervid systematics proposed by Groves (2005) and Groves & Grubb (2011) is applied in the present study. The abbreviations for measurements used in this paper: CBL, condylobasal length; L, length or distance; D, breadth or diameter; DAP, anteroposterior diameter; DLM, lateromedial diameter; Pr, prosthion; Na, nasion; Br, bregma; Op, opisthocranion; Bs, basion; Or, orbit; Pd, pedicle; PP, premolar series; MM, molar series.

3. Systematic description of the family Cervidae Goldfuss, 1820

3. 1. Subfamily Capreolinae Brookes, 1828

3. 1. 1. Genus *Cervavitus* Khomenko, 1913

Khomenko (1913) described three cervid forms from the Late Miocene of Taraclia (Moldova): *Cervavitus tarakliensis* (based on two-tined small antlers), *Cervoceros novorossiae* (based on an antlered frontlet with asymmetric antlers: the two-tined right antler and the three-tined left antler), and *Damacerus bessarabiae* (based on an antlered frontlet with palmed antlers). Zdanski (1925), who acted as the first reviewer, considered only two Khomenko's genera as valid: *Cervocerus* and *Cervavitus*, while *Damacerus* was regarded as a junior synonym of *Cervocerus*. According to Pidoplichko & Flerov (1952), all Khomenko's genera are synonymous and the priority is given to *Cervavitus*. Azzaroli (1953: p. 9) considers all cervid species from Taraclia as synonyms and chose *Damacerus bessarabiae* as a senior synonym since this combination of species and genus names are based on fully grown mature antlers,
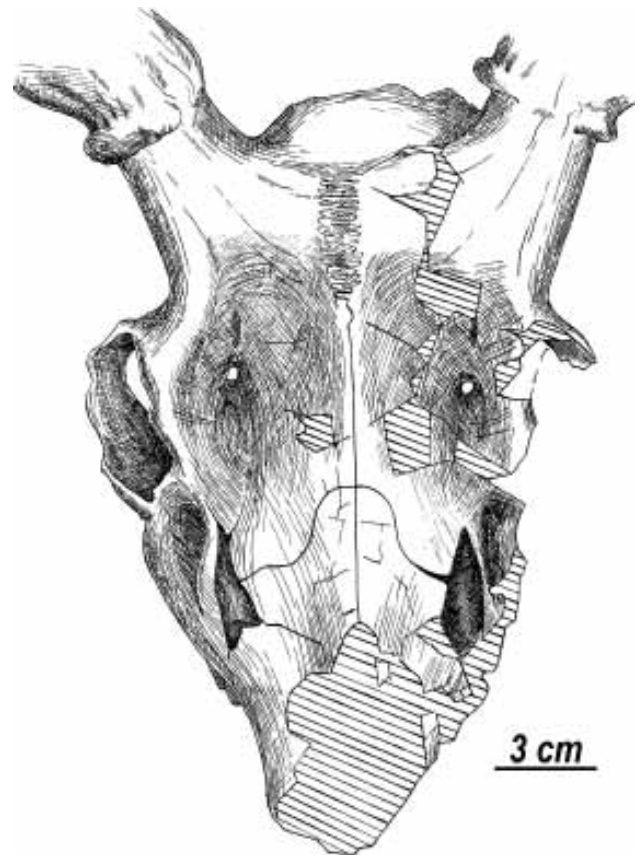

Figure 1: *Cervavitus variabilis* Alekseev, 1915: the frontal view of the skull of Nr. 43-1612 (MNHK) from Novoelizavetovka, Ukraine (antlers are not shown).

but this point of view cannot be accepted because of the earlier established priorities (see the discussion of this case in Grubb 2000). Azzaroli (1953) suggests that "*Cervocerus novorossiae*" from China represents similarly primitive, but completely different cervid form, characterized by larger size, with always cylindrical three-pointed antlers, primitive lower fourth premolar (P^4), and the absence of *Palaeomeryx* fold in lower molars. According to Azzaroli (1953), a new generic and specific name is required for the Late Miocene cervid from China. Godina et al. (1962: p. 372) designated *Procervus variabilis* Alexejev, 1913 from Late Miocene of Eastern Europe (MN 11) as a type species of *Cervavitus*. This opinion was followed by Korotkevich (1970) and Vislobokova (1990). However, according to the article 67.1 of the ICZN, the name-bearing type of the genus *Cervavitus* is *Cervavitus bessarabiensis* Khomenko, 1913. *Cervavitus sibiricus* Flerov (Flerov 1952: p. 134) from Pavlodar is apparently a *nomen nudum*.

Cervavitus bessarabiensis Khomenko and *Cervavitus variabilis* (Alexejev) from Eastern Europe are two phylogenetically related primitive cervid forms representing similar stages of cervid evolution. They share the same basic plan of antler construction (the basal tine with variable height of insertion and dichotomously branched distal part of beam) and the presence of *Palaeomeryx* fold in lower molars. However, *Cervavitus variabilis* is more advanced in

Figure 2: *Cervavitus variabilis* Alekseev, 1915: the outline of right antler the specimen Nr. 43-1612 (MNHK) from Novoelizavetovka, Ukraine.

rather short, robust, somewhat compressed antero-posteriorly, and oriented toward the posterior and laterally pedicles and more heavy antlers with frequent supernumerary tines (Fig. 1). The fully grown antlers of *Cervavitus variabilis* are flattened and often have additional tines in distal part, while the basal tine may often be bifurcated (Fig. 2). The frontal bones of the antlered skull Nr. 43-1612 (MNHK) of *Cervavitus variabilis* from Novoelizavetovka (Ukraine) are some-what concave between the orbits and a little convex behind the orbits. The posterior edge of nasal bones is rounded and does not reach the imaginary line connecting anterior edges of orbits. The orbitofrontal part of the skull is short: the anterior edge of orbits is situated above the anterior part of M^2. The preorbital pits are very deep and large and attain 70% of the orbit's horizontal diameter. The dentition morphology of *Cervavitus variabilis* is peculiar: the upper canines are present and they are very large saber-like in males; the P_4 is molarized; the lower molars are characterized by presence of the *Palaeomeryx* fold; the lower premolar series is rather long (the mean premolar/molar ratio amounts to 68%). The "*Palaeomeryx* fold" of upper molars reported by Korotkevich (1970: p. 55), apparently, is an accessory enamel fold of protocone ("bifurcated protocone"). The differences in pedicle morphology

and molarization of P_4 between *Cervavitus bessara-biensis* and *Cervavitus variabilis* might be estimated as taxonomical criteria at the genus level, if one applies the same taxonomic criteria as for other cervid groups (for instance, in the case of modern *Cervus* and *Dama*). The genus name *Procervus* Alexejev, 1913 is not available, since it is preoccupied by *Procervus* de Blainville, 1840 and *Procervus* Hodgson, 1847 (Grubb 2000). Schlosser (1924) proposed the genus name *Metadicrocerus* for *Procervus variabilis* Alexejev 1913 that seems to be an available taxonomical solution.

Khomenko (1913) placed the primitive deer from Taraclia in a new taxonomic group "Pliocervini" and assumed their intermediary position between primitive munjac-like deer and advanced modern cervids. According to Khomenko (1913), *Cervavitus* is characterized by a mixture of advanced cervid (subfamily Cervinae) characters (large body size, large branched antlers), primitive *Muntiacus*-like characters (large upper canines in males, long pedicles, large preorbital pits, bony ridges connecting the pedicles with orbits), and general cervid plesiomorphic characters (the holometacarpal condition of limbs, the *Palaeomeryx* fold in lower molars). The frontal bones, as I could see in the skull Nr. 43-1612 (MNHK) from Novoelizavetovka (Fig. 1), are some-what depressed between orbits, but there are no any clear bony ridges on the lateral sides of frontal bones reported by previous authors. The frontal bones of the specimen Nr. 43-1612 are characterized by a presence of smoothly rounded lateral ribs that connect orbit with pedicle base, as in modern large-sized cervids, but this morphological condition does not remind the shape of frontal bones of *Muntiacus*. However, the assumed transitional morphology of *Cervavitus* between "primitive" muntjacs and advanced Cervinae was accepted uncritically by consecutive authors (Flerov 1952; Azzaroli 1953; Godina et al. 1962; Korotkevich 1970; Vislobokova 1990; Petronio et al. 2007). The so-called "frontal bony ridges" in *Cervavitus* most probably are not homologous to the frontal bony ridges in *Muntiacus*. In modern *Muntiacus* (also called "rib-faced deer"), the sharp frontal bony ridges extend from pedicle base to nasal bone from each side of face above orbits. This specific morphology of muntjac's facial bones may be explained by the intraspecific combat behavior of males (Croitor 2001a). Since *Muntiacus* males possess the double offensive weapon (large upper canines and sharp pike-like antlers), the unpredictable behavior of a rival during the intraspecific combats increase the probability of injury, which may cause the loose of breeding opportunity or death. According to Barrette (1977), rival's tusks frequently inflict cuts to the neck, sides of the face, and the ears. Obviously, eyes are exposed to an increased danger of wounding during the intraspecific combats. The bony ridges situated immediately above the eye sockets form a likeness of groove that prevent the

lateral slide of rival's tusks and perform a protection function of eyes during the combats (Croitor 2001a). Among primitive tusked deer, the frontal bony ridges are recorded only in modern *Muntiacus* and therefore must be regarded as a specific apomorphic character of this genus. Its adaptive significance may be explained by peculiar for *Muntiacus* backward orientation of long thin pedicles which do not ensure the protection of eyes, as, for instance, in *Heteroprox* characterized by the vertical position of pedicles immediately above eye sockets, the presence of large tusks and the absence of facial bony ridges (Azanza et al. 1989: fig. 5). Apparently, one can see the analogy of protecting frontal bony ridges in *Protoceras* armed with large upper canines and complicate facial horn-like structures and bony ridges above eyes. Therefore, I do not see any clear support for Khomenko's hypothesis on *Cervavitus* from Eastern Europe as a phylogenetical link connecting muntjacs and modern Cervinae.

Zdansky (1925) reported the presence of *Cervavitus novorossiae* in Late Miocene of China. Teilhart de Chardin & Trassaert (1937) described from Late Miocene of Northern China a new subspecies *Cervavitus novorossiae demissus*. Dong (2011) suggests that *Cervavitus novorossiae demissus* is synonymous with *Cervavitus shanxius*. If this is true, *Cervavitus novorossiae shanxius* Dong & Hu 1994 is a junior synonym of *Cervavitus novorossiae demissus* Teilhart de Chardin & Trassaert 1937 according to the principle of priority. Dong & Hu (1994) reported some differences between *Cervavitus novorossiae* from Taraclia and "*Cervavitus novorossiae*" from Shanxi: the Chinese form is characterised by shorter pedicles and missing *Palaeomeryx* fold in lower molars. Many authors agree that the Chinese cervid remains hardly represent the same deer form as *Cervavitus* from Late Miocene of Eastern Europe (Azzaroli 1953, 1992; Czyżewska 1968; di Stefano & Petronio 2002). Apparently, the primitive Chinese Late Miocene and Pliocene holometacarpal deer with three-pointed antlers represent a similar to *Cervavitus* evolutionary stage, but different evolutionary branch and should be placed in a separate genus.

3. 1. 2. Genus *Procapreolus* Schlosser 1924

Schlosser (1924) proposed the genus *Procapreolus* for poor remains of three-pointed cervid antlers of *Cervus* (*Palaeaxis*) *loczyi* Pohlig 1911 from Late Miocene of Pannonia and included in the new genus two other Neogene cervids *Cervavus rutmeyeri* Schlosser 1903 and *Procapreolus latifrons* Schlosser 1924 from Mongolia. Korotkevich (1963, 1965b), the first reviewer of the genus, designated *Procapreolus latifrons* as the type species. Korotkevich (1963, 1965b) also noticed the distinct shape of antler of *Procapreolus rutmeyeri*, which does not correspond to the assumed typical for the genus roe deer antler morphology, and excluded this species from *Pro-*

capreolus. According to the reasonable remark of Gentry (2005), the genus name *Procapreolus* seems to refer to *Procapreolus loczyi* too, which was ignored by Korotkevich (1963). Furthermore, Korotkevich (1965b) and Czyżewska (1968) suggest that the antler shape of *Cervus* (*Palaeaxis*) *loczyi* shows a similarity 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 some-what closer to the burr than to the second ramification. The antler is some-what compressed from the sides and reminds to a certain extent *Cervavitus novorossiae*. One of pedicles figured by Pohlig (1911) is rather thin and long, but another pedicle connected to a small part of antler is rather short and robust. The figured specimens come from various localities and apparently belong to different cervid forms. Finally, according to Dong &Ye (1997), *Procapreolus latifrons* is a random variation form of *Cervavitus novorossiae* Khomenko from China. Possibly, the genus *Procapreolus* in its current understanding is a polyphyletic taxon.

Korotkevich (1963) also included in *Procapreolus* her new species *Procapreolus ucrainica* (later emended for *Procapreolus ukrainicus* Korotkevich, 1965) from Late Miocene of Ukraine. This species is peculiar in its long and thin three-tined antlers. The position of first tine is very high, closer to the second ramification than to the burr. Its dentition is characterized by presence of cingulum and protoconal fold in upper molars and *Palaeomeryx* fold in lower molars. The antlers of *Procapreolus florovi* Korotkevich 1974 from the final Miocene of Ukraine are as in the previous species, but its dentition is characterized by the very weak *Palaeomeryx* fold, the missing cingulum of upper molars, the molarized P_4 (not known in *Procapreolus ucrainica*), and some-what diverging long pedicles (not described in *Procapreolus ucrainica*). The series of lower premolars is relatively long: the premolar to molar length ratio in two mandibles described by Korotkevich (1974) amounts to 86.1% and 81.2%. Czyżewska (1968) included in *Procapreolus* a primitive cervid *Cervocerus wenzensis* Czyżewska, 1960 from Early Pliocene of Poland. Czyżewska (1968) and Korotkevich (1970) noticed that *Procapreolus* and *Cervavitus* share similar primitive cranial morphology. Croitor (1999) included in the genus *Procapreolus* the Pliocene cervid *Cervus* (*Rusa*) *moldavicus* Janovskaya, 1954 from Moldova. The type of "Moldavian sambar deer" is a partial skeleton of a juvenile female characterized by presence of *Palaeomeryx* fold and additional protoconal fold in upper molars. Later, Croitor & Stefaniak (2009) included *Cervocerus wenzensis* Czyżewska, 1960 in the synonymy list of *Procapreolus moldavicus* (Janovskaya, 1954). Antlers and teeth of *Pliocervus graecus* Azanza, 1995 from Mio-Pliocene transition of Greece are undistinguishable from *Procapreolus moldavicus*

and *Procapreolus florovi*. Therefore, the Greek species should be included in *Procapreolus* as *Procapreolus graecus* (Azanza, 1995). Korotkevich (1970, 1988) also included in *Procapreolus* the small-sized peculiar cervid *Cervus cusanus* Croizet & Jobert, 1928 from the Pliocene of France. This small-sized cervid (the estimated body mass based on cranial and dental remains is around 30 kg) is characterized by conspicuously flattened antlers with the number of tines varying from 3 to 5, moderately long pedicles, a highly molarized P^4, and the missing *Palaeomeryx* fold in lower molars (Fig. 3). According to Valli (2010), *Procapreolus cusanus* belongs to telemetacarpal cervids, since it is characterized by peculiar for this group shape of post-glenoid foramen, which is not completely surrounded by squamosal bone and bordered in its posteromedial part by petrous bone. The fossil remains from Ukraine described by Korotkevich (1970, 1988) as *Procapreolus cusanus* should be referred to *Procapreolus moldavicus*.
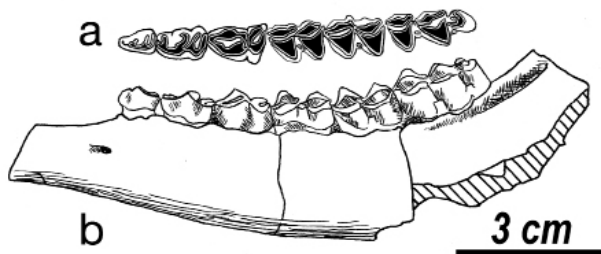

Figure 3: *Procapreolus cusanus* (Croizet et Jobert, 1828): occlusion surface of tooth row **(a)** and side view **(b)** of the left hemimandible Nr. 5237 from Etouaires, France (MNHN, Collection of Croizet).

Procapreolus moldavicus is the best known species of the genus. This is a hog-deer sized cervid with estimated body mass about 40-50 kg. Its preorbital pits are large and deep; their diameter attain 75% of diameter of orbit (Fig. 4). The preorbital pits of females are almost of the same relative size (Fig. 6). Pedicles are very long with low inclination backward and some-what diverged; their length significantly exceeds their transversal diameter. Antlers are three-pointed, the first tine is situated very high, nearly in the middle between the antler burr and the distal fork; the antler beam is slightly diverged toward the posterior in the area of first ramification; all tines are situated in the same plane. The upper canines are large and saber-shaped in males. Upper molars with accessory fold of protocone; lower molars normally with the *Palaeomeryx* fold. Lower fourth premolar (P_4) is molarized (Fig. 5). The premolar to molar series length ratio varies between 58.8% and 71.1% (Croitor & Stefaniak 2009). The known area of distribution of *P. moldavicus* ranges from the North Caucasus to the North Carpathian foothills; the stratigraphic range encompass MN14-MN15.
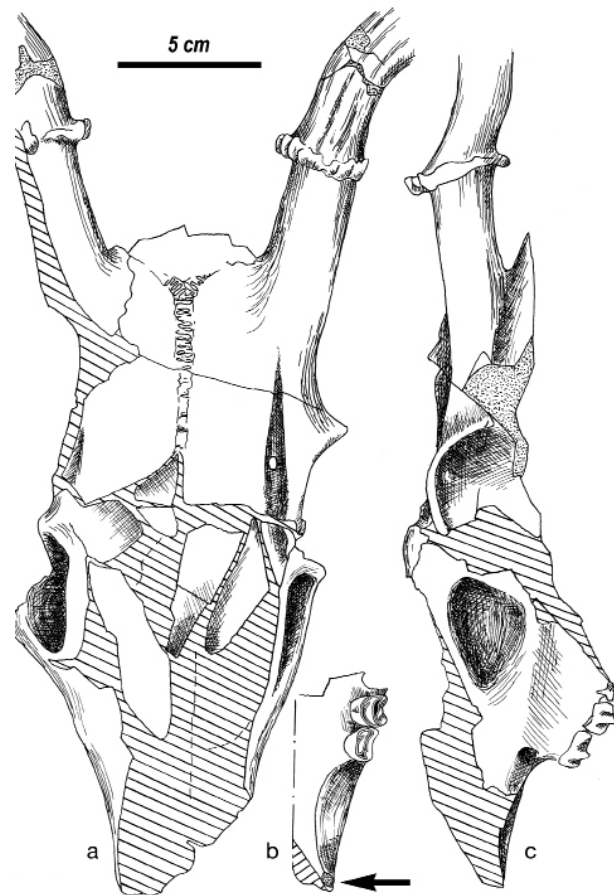

Figure 4: *Procapreolus moldavicus* (Janovskaya, 1954): the male skull (holotype of *Cervocerus wenzensis* Czyżewska, 1960) Nr. 220 (IZW) from Węże, Poland: **(a)**, superior view; **(b)**, inferior view of diastema portion and premolars; **(c)**, side view; antlers are not shown). The arrow points to the alveolus of upper canine.

3. 1. 3. Genus *Capreolus* Frisch, 1775

The modern genus *Capreolus* is a highly specialized small-sized dweller of boreal forests with specific adaptations to cold seasonal climate, 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 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, incranial, with short space between them. Nasal bones are long and extended behind the line connecting the anterior edges of orbits (Fig. 7b). Preorbital fossa is very small. Upper canines are lost as in *Alces*, representing an exception among modern Capreolinae that maintain upper canines during all their life. The protoconal fold in upper molars is reduced; the *Palaeomeryx* fold is never present. P_4 is highly molarized. The premolar/molar ratio varies around 70.5 %. Antlers are three-pointed with a well developed burr and strong pearling in their proximal part. The earliest representative of the genus, *Capreolus constantini*, is reported from
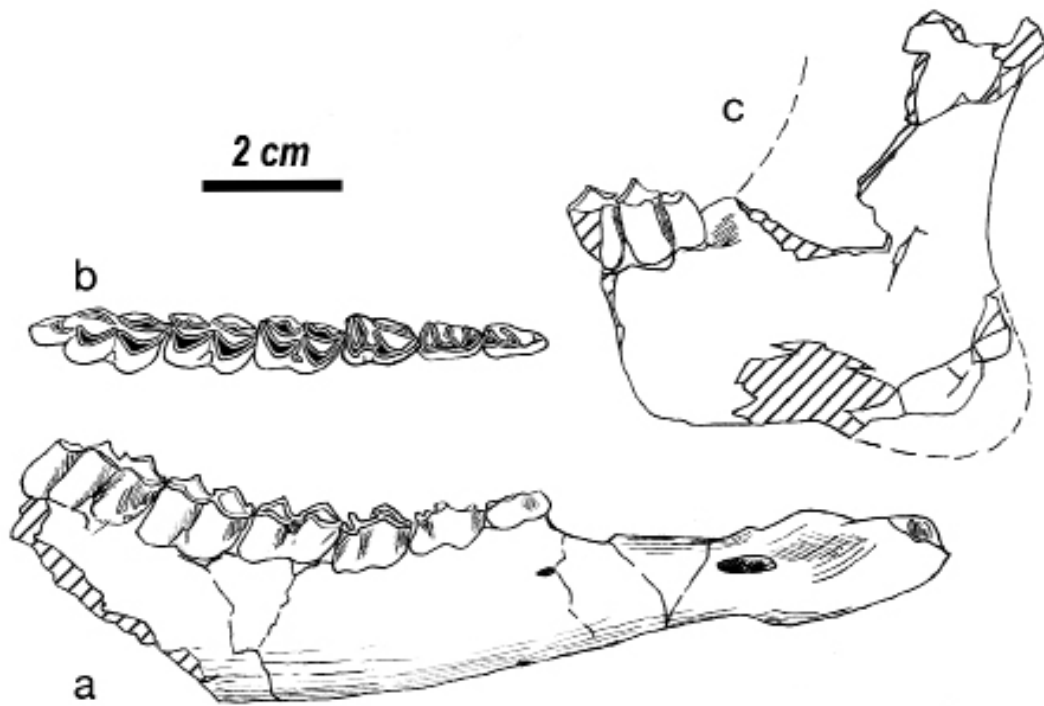
Figure 5: *Procapreolus moldavicus* (Janovskaya, 1954): the lower mandible of the specimen Nr. 220 (IZW) from Węże, Poland (**a**, side view of right mandibular ramus; **b**, occlusion surface of right lower tooth row; **c**, side view of left mandibular ramus).
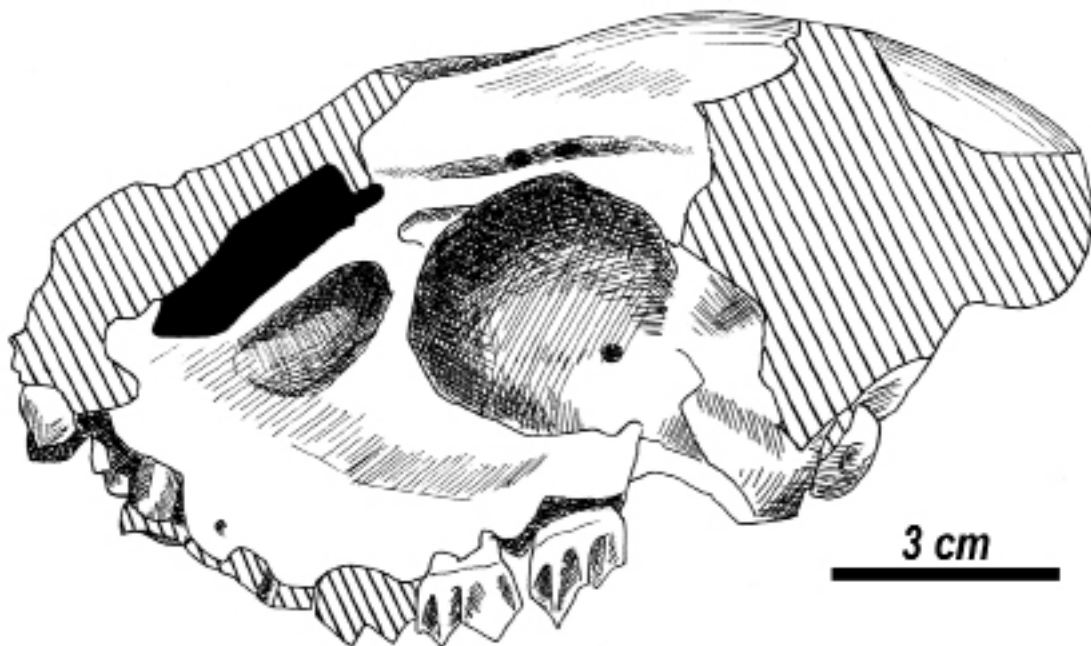

Figure 6: *Procapreolus moldavicus* (Janovskaya, 1954): the skull of juvenile female Nr. 345 (IZW) from Węże, Poland.

Pliocene (MN16) of Udunga, Trans-Baikal Area (Vislobokova et al. 1995). The earliest roe deer in Western Eurasia, *Capreolus cusanoides*, was reported by Kahlke (2001) from Untermassfeld (Germany), ca. 1.02 Ma. Kahlke (2001) noticed the great similarity of antlers of the roe deer from Untermassfeld with *Procapreolus cusanus*, however, the morphology of dentition of *Capreolus cusanoides* is similar to modern roe deer. Nonetheless, the premolar/molar series ratio in the specimen of lower mandible IQW 1993/24 360 from Untermassfeld is very primitive and amounts to 91.1% (the index is calculated according to the measurements in Kahlke 2001). Such a long premolar series approaches the roe deer from Untermassfeld to the most primitive forms of *Procapreolus*, such as *Procapreolus ucrainica*. The length of premolar series in *Procapreolus cusanus* from Perrier (France) is relatively shorter and, therefore, repre-
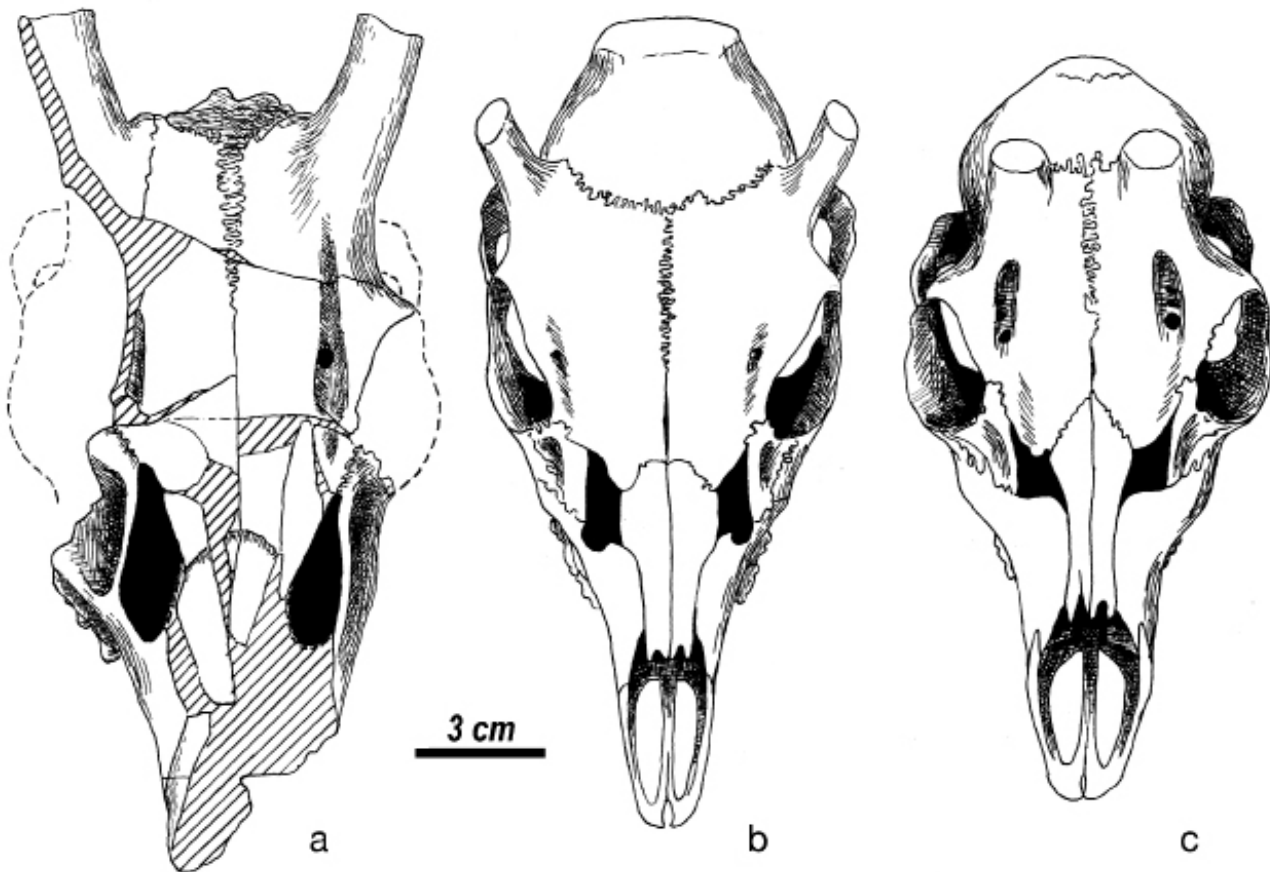
Figure 7: Dorsal views of crania of **(a)** *Procapreolus moldavicus* (Janovskaya, 1954) from Węże, Poland (Nr. 220, IZW); **(b)** *Odocoileus virginianus* (IZW); **(c)** *Capreolus capreolus* (IZW).

sents the more advanced morphological condition. The premolar/molar ratio in the specimen Nr. 5237 (collection of Croizet, MNHN) amounts to 69.3 %.

The phylogenetical and systematical close relationship between 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; di Stefano & Petronio 2002). This viewpoint rests mostly on the basic for *Capreolinae* plan of antler construction shared by *Capreolus* and *Procapreolus*. It is difficult to confirm or to reject this opinion, partly due to the high possibility of polyphyly of *Procapreolus* in its current understanding, and partly due to the fact that the best known cervid from Eastern Europe forms ascribed to *Procapreolus*, such as *Procapreolus moldavicus*, is a primitive form characterized by the plesiomorphic mixture of Muntiacine, Odocoileine, and Capreoline cranial and dental characters. The basic antler construction (the highly situated anterior tine and the dichotomously branched beam) can be seen also in modern *Ozotoceros*, *Alces*, as well as in extinct *Cervavitus*, *Eocoileus*.

3. 1. 4. Genus *Pliocervus* Hilzheimer, 1922

The definition of *Pliocervus* from Late Miocene (MN 12-13) of Europe is still confused and contradictory. According to Godina et al. (1962), *Pliocervus* is characterized by a well-developed cingulum in upper molars, the little sloped lingual walls in upper cheek teeth (correlated with advanced hypsodonty), the missing *Palaeomeryx* fold in lower molars, and the three-tined antlers with the high insertion of the first tine. The diagnosis was accepted by Czyżewska (1968) and, in general lines, by Korotkevich (1970), who, however, did not confirm the presence of cingulum in upper molars. The systematical position of *Pliocervus* with vague and unclear diagnosis remained unclear, however tentatively it was placed in the subfamily Cervinae grouped with holometacarpal *Cervavitus* in the tribe Pliocervini (Czyżewska 1968; Vislobokova 1990; Azanza 2000). According to the reasonable opinion of Gentry (2005), the distinction between *Pliocervus* and *Procapreolus* is inadequate. This confusion, apparently, occurred because remains of *Procapreolus* often were ascribed to *Pliocervus* (Croitor & Stefaniak 2009).

The type species *Pliocervus matheronis* (Gervais, 1859) is similar in body size to modern roe deer, but its antlers are relatively larger. The holotype (antlered frontlet) from Mont Luberon (Cucuron, France) is characterized by narrow frontal bones (frontal breadth amounts to 74 mm) and more or less parallel orientation of rather long (L>D) but robust pedicles
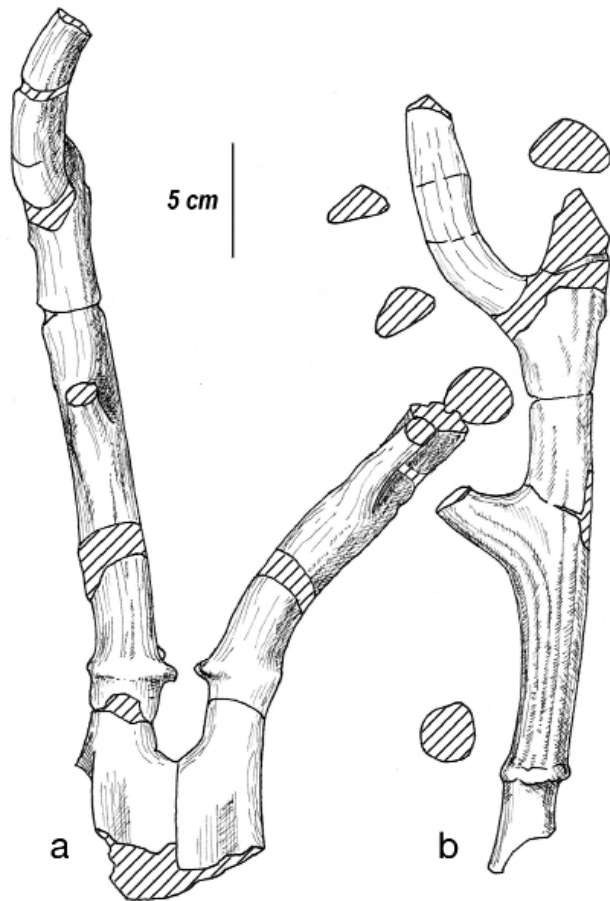
Figure 8: *Pliocervus matheroni* Gervais, 1859: the antlered frontlet from Cucuron (France), holotype **(a)**, frontal view; **(b)**, median view of the right antler).

situated very close each from another as in *Capreolus*, the backward inclination of pedicles is very low (Fig. 8). The antlers are characterized by a high position of the first tine and the second tine inserted on the anterior side of the beam; the cross-section of the antler beam is sub-triangular. The sample from Mont Luberon also contains distal fragments of antlers with second tine and distal bifurcation, therefore the fully developed antlers of *Pliocervus matheronis* are four-tined. Upper molars are supplemented with the protoconal fold; the hypoconal spur and cingulum are not present. The entostyle in upper molars is very weak; the lingual wall in upper cheek teeth is sloped. The fourth lower premolar (P_4) is not molarized and retains a primitive morphological condition. The *Palaeomeryx* fold is hardly visible, but present. The series of lower premolars is rather long; premolar to molar length ratio amounts to 66.3 %. Gentry (2005) mentioned a left upper canine from Mont Luberon (stored in NHML) that probably belongs to *Pliocervus matheronis*. The main morphological characters of dentition, antlers and orientation of pedicles of *Pliocervus matheronis* are quite similar to Late Miocene *Pavlodaria orlovi* from the *Hipparion* fauna of Pavlodar, Kazakhstan. Korotkevich (1970) has already expressed a reasonable opinion on a

similar pattern of antler construction of *Pavlodaria orlovi* (= *Cervavitus orlovi* fide Korotkevich 1970: 62) and *Pliocervus matheronis*. The cervid from Pavlodar is distinguished only by more advanced morphology of the molarized P_4 and flattened antlers. Vislobokova (1980), taking in consideration the basicranial morphology, regards the deer from Kazakhstan as the earliest representative of the New World cervid lineage. The genera *Pliocervus* Hilzheimer, 1922 and *Pavlodaria* Vislobokova, 1980, therefore, must be very close or even synonymous. This observation is very important, since it implies the belonging of *Pliocervus* to the subfamily Capreolinae. Obviously, the genus *Pliocervus* should be restricted to the type species *Pliocervus matheronis* (if we keep *Pavlodaria* as the separate genus). Azanza (2000) indicates the divergent pedicles in *Pliocervus* as a differential diagnostic character, which contrasts with the parallel pedicles of *Procapreolus*. This statement is erroneous, since the type material from Cucuron shows a parallel orientation of pedicles in *Pliocervus matheronis*, while the pedicles of *Procapreolus moldavicus* from Weże are rather divergent as in modern *Odocoileus* (Fig. 7). The antlers of *Pliocervus kutchurganicus* Korotkevich, 1965 from Early Pliocene of Ukraine fall in the range of individual variation of *Procapreolus moldavicus* and therefore those two species names are synonymous (Croitor & Stefaniak 2009). "*Pliocervus*" *pentelici* (Gaudry, 1865) is a problematic species from the Late Miocene of Greece (Pikermi, MN 12). The original description of species by Gaudry (1865) reports a braincase and fragments of lower mandible. The braincase with inflated large bulla tympani PIK2020 (MNHN) belongs to a bovid. The fragments of lower mandibles belong to a very small deer similar in size to modern *Muntiacus* and *Hydropotes*. These specimens are characterized by primitive P_4 and a very weak *Palaeomeryx* fold. According to Kostopoulos (2006), the small-sized cervid mandibles from Pikermi belong to the genus *Lucentia* Azanza & Montoya 1995. Azanza et al. (2013) point out that the size of smaller teeth is rather similar to *Cervavitulus mimus*. The antlers from Pikermi belong to another deer of larger size *Procapreolus graecus* (Azanza 1995). *Pliocervus turoliensis* (Azanza, 2000) is based on very poor remains of antlers and pedicles, which do not show clear characters of the genus *Pliocervus*. Another poorly known species is "*Pliocervus*" *karabastuzikus* Abdrakhmanova, 1974 from Eastern Kazakhstan based on a two-tined antler that does not show any vague resemblance with *Pliocervus matheronis*. Obviously, Abdrakhmanova (1974) followed Korotkevich's (1970) diagnosis of *Pliocervus* based on misinterpreted remains of *Procapreolus*.

3. 1. 5. Genus *Alces* Gray, 1821

Elks (term here used meaning the crown group including the genus *Alces*) represent a morphologi-

cally well outlined group of few easily recognizable forms with a series of specific apomorphies as the directed sidewards pedicles, the horizontally oriented more or less long antler beams and the normally developed distal palmation of antlers. The problem of taxonomy of elks is still debated. 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. Azzaroli (1985) and Breda (2001) included all fossil elks in the genus *Cervalces*. 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 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 and unlike endemic American telemetacarpal cervids, approaching with this combination of characters to *Capreolus* and *Hydropotes* (Brooke 1878). The most peculiar cranial characters of modern elks, such as the short nasal bones, the extremely long praemaxillae and the lost contact between praemaxillae and nasals, are apomorphic characters (Breda & Marchetti 2005). The nasal bones are rather long and articulated with the praemaxillae in the oldest known elk species *Alces gallicus*, in the extinct Holocene *Alces scotti* from North America (Azzaroli 1985), as well as in the less specialized subspecies of modern elk *Alces alces caucasicus* Verestchagin 1955 (now extinct). 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). Upper molars are supplemented with protoconal fold, which still can be seen in M^3 of modern *Alces alces* (Lydekker 1915: p. 231, fig. 35). Lower premolars P_3 and P_4 are highly molarized. 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 modern *Alces alces* stored in the NHML, and the premolar/molar ratio of all known complete lower tooth rows of *Alces gallicus* and *Alces latifrons* falls within this range of variation. Azzaroli (1952) reported the presence of a week *Palaeomeryx* fold in lower molars of the holotype of *Alces gallicus* from Seneze, however, Heintz & Poplin (1980) and Breda (2001) disproved this statement. Nonetheless, I confirm that the weak *Palaeomeryx* fold is present in M_1 and M_2 of the specimen M6227 (the holotype of *Libralces minor*

Azzaroli, 1953). The broad terminal antler palmation is the most peculiar character of the genus; however, this character is not constant and varies within the modern species *Alces alces*, 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 also recorded in other subspecies as individual variants. The degree of development of palmation in elks depends of the individual age, the nutrition quality, and the physical state of animal (Flerov 1952). The general plan of unpalmed elk antlers reminds the basic antler type of Capreolinae (Fig. 9). The general antler construction in *Alces* is characterized by development of main 3-5 tines: the basal tine is directed toward the anterior, often is double or bifurcated; the antler beam is bent toward the posterior in the area of basal bifurcation and in the simplest case is terminated by a fork, but supernumerary tines are often present on the anterior side of the beam (if the antler is oriented in the vertical plane). This "basic" type of antler is also seen in *Cervavitus*, *Pliocervus*, *Capreolus*, *Procapreolus*, and the earliest American cervid *Eocoileus*. The evolutionary modifications of 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 antler (between the burr and the basal ramification), which is extremely long in the oldest known Villafranchian species *Alces gallicus*.
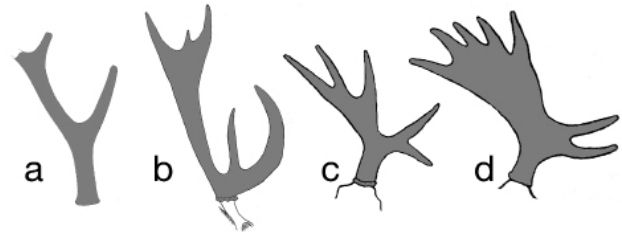

Figure 9: Antler shape in Capreolinae: **(a)** *Procapreolus loczyi* (adapted from Zapfe 1997), **(b)** *Cervavitus variabilis* (43-1612, MNHK), **(c-d)**, *Alces alces* (adapted from Boeskorov 2001).

The origin of elks remained unclear. The phylogenetical lineage of elks could be traced in the paleontological record only from Early Pleistocene (Heintz & Poplin 1980; Breda & Marchetti 2005). Vislobokova et al. (1995) reported a poor fragment of a similar to typical elk frontal bone from Pliocene of Udunga, Trans-Baikal Area. Flerov (1952: 13) regarded *Eucladoceros* as a possible forerunner of *Alces*, but this viewpoint was not supported. Dental and postcranial remains from Pontian of Moldova described as *Alces maeoticus* Pavlow, 1926 actually belong to a giraffid *Palaeotragus* (Heintz & Poplin 1980). *Pseudalces mirandus* Flerov, 1962 from the mixed fauna of Villafranchian type of Kosiakinskiy Quarry, most probably, is close to or even synonymous with giant *Arvernoceros verestchagini* David, 1992 (Croitor

2005, 2009). *Tamanalces caucasicus* Vereshchagin 1957 from Quaternary fauna of Tamani is based on a poor fragment of frontal bone with pedicle and most probably is a junior synonym of *Praemegaceros solilhacus* (Croitor 2006b).

3. 2. Subfamily Cervinae Goldfuss, 1820

3. 2. 1. Genus *Praeelaphus* Portis, 1920

Portis (1920: 133) proposed the subgenus *Cervus* (*Praeelaphus*) for Early Villafranchian species *Cervus arvernensis* Croizet & Jobert, 1828, *Cervus perrieri* Croizet & Jobert, 1828, and *Cervus etueriarum* Croizet & Jobert, 1828 from Perrier (France). According to Heintz (1970), *Cervus etueriarum* is based on a juvenile specimen of *Cervus perrieri*. The species *Cervus arvernensis* was based on a poor fragment of antler with low insertion of the basal tine and with some reservations was included by Lydekker (1885: p. 115) in the synonymy of *Cervus polignacus* Robert, 1830 (= *Dama clactoniana*: Croitor et al. 2006), but most probably it also falls within the individual variation of *Cervus perrieri*. Another poorly known species, *Cervus issiodorensis* Croizet & Jobert 1828, is represented by the shed antler Nr. 211214 (PMUL) characterized by a rather low insertion of the short and laterally compressed basal tine and the pyriform shape of the beam cross-section. This species is also a junior synonym of *Cervus perrieri*. Heintz (1970) placed *Cervus perrieri* in the arbitrary group *Cervus sensu lato*; therefore the question of its systematical position remained open. Croitor (2012) chose *Cervus perrieri* as genotype of *Praeelaphus* and included in this genus *Pseudodama lyra* Azzaroli, 1992 and *Cervus warthae* Czyżewska, 1968. Grubb (2000) supposed that *Praeelaphus* Portis may be synonymous with *Metacervocerus* Dietrich, however, this is not the case: those taxa are based on two different recognized valid species: *Cervus perrieri* and *Cervus pardinensis* respectively. The proposed diagnosis of *Praeelaphus* is the following: deer of intermediate body size between modern European red deer and fallow deer. Pedicles of moderate length (median length of pedicle in adult males normally does not exceed its diameter), compressed anteroposteriorly. Fully grown antlers are large, four-pointed. The first tine normally is situated above the burr at a distance larger than diameter of the antler base. The antler segment between the first and the second tines is significantly longer than the segment between the second tine and the distal bifurcation. The antler beam forms flattened extensions in the areas of ramification. The transversal section of beam below the second tine is not regular, often pyriform. The beam above second tine is significantly compressed anteroposteriorly and forms an extended flattening with frontal orientation. The distal bifurcation is oriented in the frontal plane. The dentition is primitive: P_4 is simple, with low degree of molarization, the lower premolar series is relatively long, longer than in *Cervus* and *Dama* (Croitor 2012). 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 by antler morphology and are characterized by the same body size (around 180 kg). At least, 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) from Early Villafranchian deposits of Lower Valdarno (Italy) is very close to *Praeelaphus perrieri*. The holotype of *Praeelaphus lyra* is an antlered frontlet IGF1933v from Ponte a Elsa (Azzaroli 1992: p. 7, fig. 2; pl. 1-1 a-c). The antlers, apparently, did not achieve their full degree of development: they are characterized by specific flattening of the distal beam segment, but the distal bifurcation is not developed yet. An initial distal bifurcation is present only on the left antler. 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. Pedicles are comparatively longer than in *Praeelaphus perrieri*, indicating the young individual age of the type specimen of *Praeelaphus lyra* (see Tab. 1). The latest remains of a cervid very similar to *Praeelaphus lyra* from Ponte a Elsa comes from Olivola, a Late Villafranchian site (1.8 Ma) in Tuscany. The antlered braincase IGF1378 of *Praeelaphus* cf. *lyra* from Olivola was reported by Azzaroli (1947: p. 52, fig. 1-7; p. 55, fig. 4-1) as *Dama nestii nestii*. This specimen is characterized by a set of distinguishing from *Dama* characters: the rather long pedicles are inclined backward; the braincase is quite long with just slightly convex parietal bones, the basioccipitale is bell-shaped and broadened in the area of pharyngeal tuberosities (Fig. 10). The distal portion of antler is destroyed, but one can assume that the total number of antler tines is four. The antler beam above the second tine is extended into a blade-like flattening, oriented in a frontal plane, transversally to the plane of the second tine, as in *Praeelaphus perrieri* and *Praeelaphus lyra*.

The earliest remains of *Praeelaphus* come from Early Pliocene of Eastern Europe. The poor antler remains of a fallow deer sized cervid from Early Pliocene sites Cociulia and Lucesti, Moldova (MN15) should be ascribed to *Praeelaphus lyra* (Croitor & Stefaniak 2009). Another cervid form, *Praeelaphus warthae* from Węże (MN15), Poland, is slightly smaller than *Praeelaphus perrieri*. The mean estimated body mass amounts to 120 kg; the body mass of a larger male was around 140 kg. The species is presented by poor cranial and antler fragments. It is characterized by sloped backward pedicles, slightly convex parietal bones, a short orbitofrontal part of skull (the anterior edge of orbit is situated above
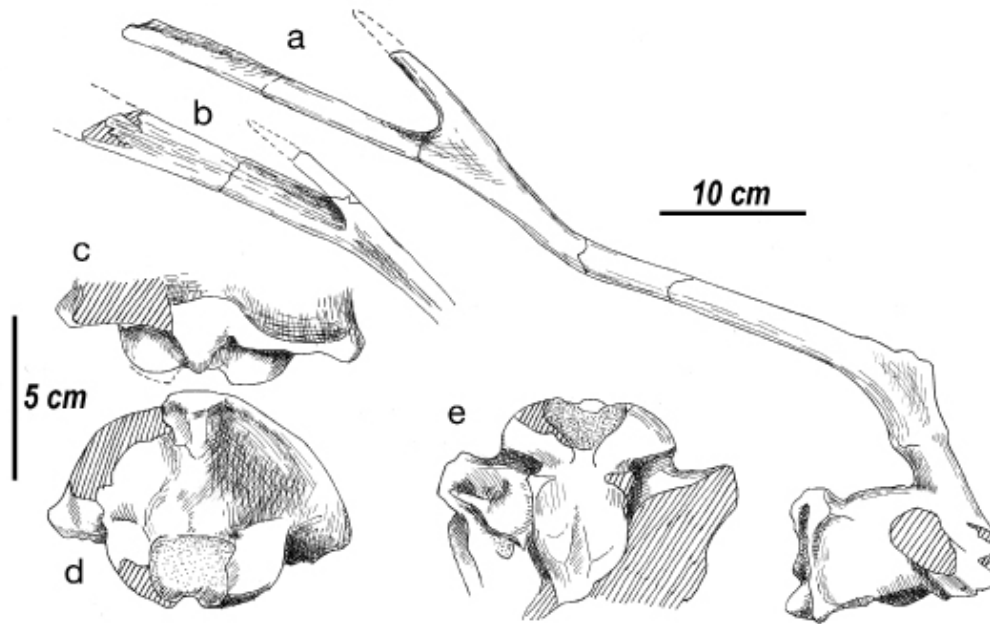
Figure 10: *Praeelaphus* cf. *lyra* (Azzaroli, 1992): the antlered braincase IGF1378 from Olivola, Italy **(a)**, side view; **(b)**, anterior view of the distal part of left antler; **(c)**, upper view of the occipital profile; **(d)**, posterior view of the braincase; **(e)**, basioccipitale view of the braincase). Note the bell-shaped basioccipitale broadened at the level of pharyngeal tuberosities.
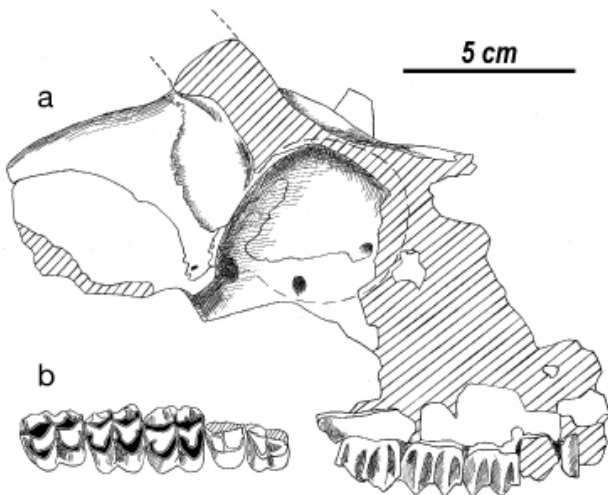

Figure 11: *Praeelaphus warthae* (Czyżewska, 1968): the skull Nr. 1 (IZW), holotype, Węże, Poland **(a)**, side view of skull; **(b)**, occlusion surface of right upper tooth row).
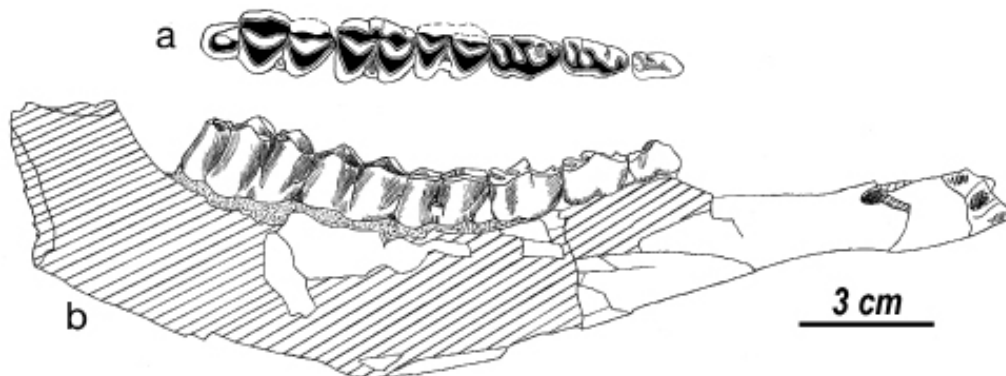
M^2/M^3), and a peculiar shape of frontal bones: convex between pedicles and depressed between orbits (Fig. 11). The anterior part of each frontal bone is swollen. Preorbital pits (fossa) are deep, but not large. Upper M^2 and M^3 are supplemented with a small protoconal fold and hypoconal enamel spur. Lower premolar series is relatively long: the premolar/molar ratio varies from 64.9% to 67.1%. P_4 is not molarized and maintains a primitive morphological condition (Fig. 12). Complete antlers are not known, but the available antler fragments suggest that generally their morphology is very similar to *Praeelaphus perrieri*. I do not exclude the possibility of synonymy of species names *perrieri, warthae*, and *lyra*, which, in fact, represent quite similar synchronous cervid forms.

Di Stefano & Petronio (2002) regard *Praeelaphus perrieri* and *Praeelaphus warthae* as the earliest pri-

Figure 12: *Praeelaphus warthae* (Czyżewska, 1968): lower mandible Nr. 363 (IZW), Węże, Poland **(a)**, occlusion surface of tooth row; **(b)**, side view).

mitive representatives of the true genus *Cervus* in Europe. There are no doubts that *Praeelaphus* represents an early evolutionary stage of cervines with advanced four-tined antlers, however, there are no evidences that this lineage is directly related to *Cervus*. Unlike *Cervus* and its closely allied genera *Panolia* and *Rusa*, *Praeelaphus* is characterized by a broad bell-shaped basioccipitale. Antlers of *Praeelaphus* are specialized, with apomorphic frontally oriented flattening of their distal beam segments. The genus *Praeelaphus* includes archaic Pliocene and Early Pleistocene deer from Western Eurasia with rather advanced antler morphology and primitive *Rusa*-like cranial morphology and most probably represents a side branch of the earliest evolutionary radiation of the Cervinae group.

3. 2. 2. Genus *Metacervocerus* Dietrich, 1938

The type species *Metacervocerus pardinensis* (Croizet & Jobert, 1828) is a fallow-deer sized cervid (the estimated body mass is about 60 kg) with simple three-pointed antlers from Pliocene (MN15-16) of Europe (Heintz 1970; Croitor & Stefaniak 2009).
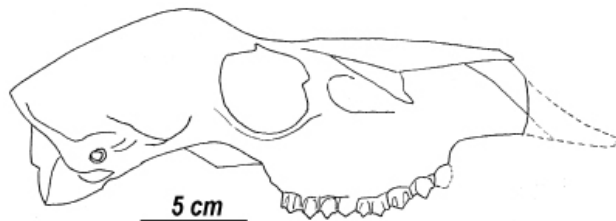

Figure 13: *Metacervocerus rhenanus* (Croizet & Jobert, 1828): the female skull Nr. 210638 from Sénèze, France (PMUL).

The first antler tine is always situated at a long distance from the burr that exceeds the DAP of the antler base. The distal bifurcation is set in the parasagittal plane; the posterior tine of distal bifurcation is always stronger and longer than the anterior one. The pedicels are long (L>D) and sloped backward as in modern *Hyelaphus* or *Rusa*. The dentition is rather primitive: upper molars with strong cingulum and very oblique lingual wall. The angle between lingual and labial walls in M^2 is wider than 40°. The morphology of P_4 is simple. Lower molars have no *Palaeomeryx* fold. Skull morphology of *Metacervocerus pardinensis* is not known, however, some fine complete crania of younger Early Pleistocene species *Metacervocerus rhenanus* (MN17-18) are available (Croitor 2006a). The skull of *Metacervocerus rhenanus* is generally primitive (Fig. 13). Its orbito-frontal region is short; the anterior edge of eye sockets reaches the level of M^2. The braincase is a little flexed and elongated. The size of orbits is normal. The bulla timpani are rounded, but not as large as in *Dama*. The basioccipital bone is broadened at the level of pharyngeal tuberosities. Upper canines are not present. The size of preorbital pits and ethmoidal openings are of moderate size. The nasal bones are rather long and are extended behind the imaginary line connecting the anterior edges of the orbits. The face length measured from the anterior edge of orbits to *prosthion* amounts to 56.9% of the condylobasal length and is relatively longer than in *Hyelaphus porcinus* and *Cervus nippon* (Croitor 2006a). The general proportions of the skull are very close to modern *Axis axis*, with exception of shorter frontal suture and long extended backward nasal bones. *Metacervocerus rhenanus* is distinguished from the
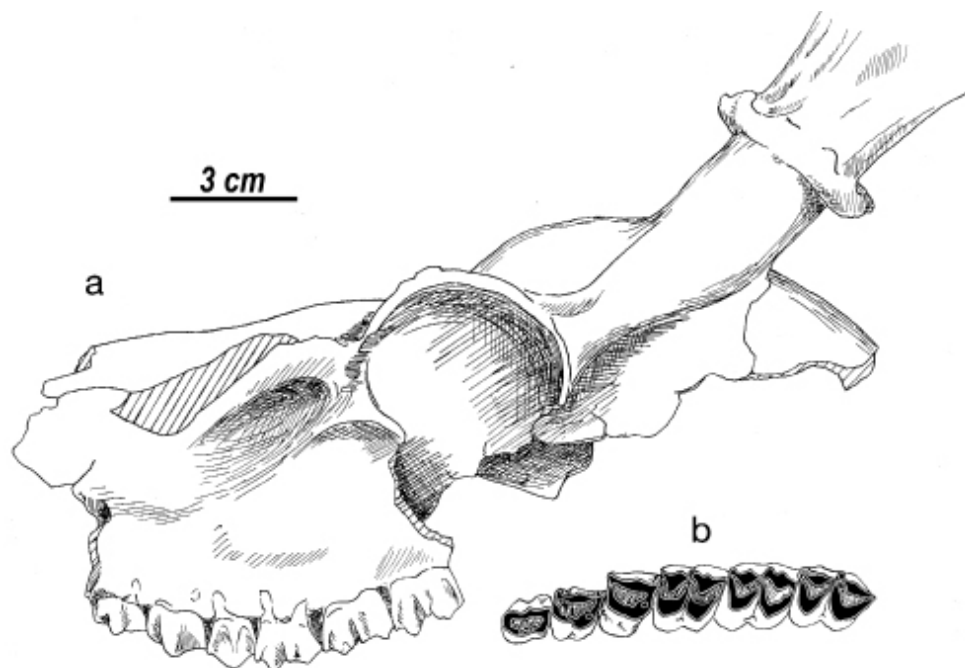

Figure 14: *Metacervocerus rhenanus* (Croizet & Jobert, 1828): the male skull CEY2-2318 (MNP, antlers are not shown) from Ceyssaguet, France **(a)**, side view; **(b)**, occlusion surface of the left tooth row).
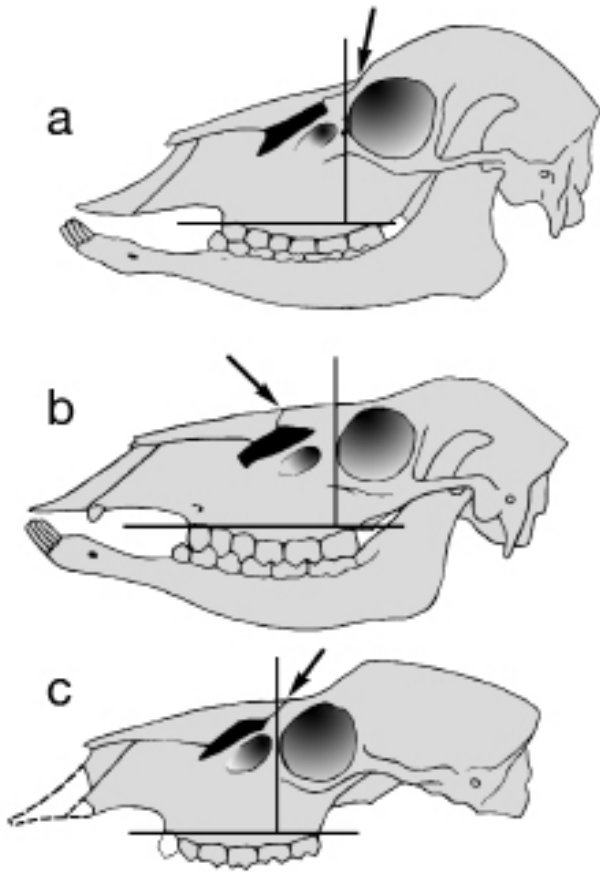
Figure 15: Skull shape in medium/small-sized cervids: **(a)** *Dama dama* (adapted from Sokolov 1959), **(b)** *Cervus elaphus* (adapted from Sokolov 1959), **(c)** *Metacervocerus rhenanus* (210638, PMUL).

type species by reduced or completely lost cingulum in upper molars and broader angles of antler ramifications. *Metacervocerus punjabiensis* (Brown, 1926) from Siwaliks of Indian subcontinent should be mentioned here because of its strong affinity with European forms in antler morphology. Brown's (1926) species is some-what larger and is characterized by comparatively higher-crowned cheek teeth.

There are several conflicting opinions about the systematical position of the cervids under discussion. 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 *Metacervocerus rhenanus* is too primitive to be included in *Dama* or *Cervus*. Unlike *Dama dama*, pedicles of *Metacervocerus* are longer and sloped backward (Fig. 14), the braincase is relatively long, little flexed bulla tympani are relatively smaller. Unlike *Cervus elaphus*, *Metacervocerus* is characterized by a relatively longer braincase and shorter orbitofrontal portion, relatively longer nasal bones, which are extended behind the line connecting anterior edges of orbits, a broad bell-shaped basioccipitale, larger bulla tympani and missing upper canines (Fig. 15). Di

Stefano & Pentronio (2002) included *Metacervocerus rhenanus* and *M. pardinensis* in the modern genus *Rusa*; however, this viewpoint is unacceptable too. Unlike *Metacervocerus*, *Rusa* is characterized by short nasal bones, which do not reach the level of anterior margins of orbits, small bulla tympani, narrow basioccipitale (as *Cervus*), and possess 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.

3. 2. 3. Genus *Arvernoceros* Heintz, 1970

This genus appears in Late Ruscinian (MN15) of Eastern Europe (Croitor & Stefaniak 2009) and in Early Villafranchian (MN16) of Western Europe (Heintz 1970). Vislobokova (2012) considers that the shed antler from Villafranchian deposits of Slobozia Mare, Moldova, originally described as *Arvernoceros ardei* (Croitor 2009: fig. 2), belongs to *Praeelaphus perrieri*, however this opinion is deniable: the antler from Slobozia Mare is characterized by a circular cross-section of beam, unlike the irregular pyriform shape of transversal section of beam seen in *Praeelaphus perrieri*. The type species *Arvernoceros ardei* (Croizet & Jobert) is still an imperfectly known medium-large cervid (the estimated body mass is ca. 170 kg) with large, but little branched antlers and primitive dentition. The general construction plane of its antlers is simple: the first basal tine is situated high above the burr, may be some-what 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. 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 phyletical 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 *Arvernoceros ardei* and *Praeelaphus perrieri*. Nonetheless, one can assume that *Arvernoceros ardei* is characterized by simple unmolarized P_4 and relatively long series of lower premolars. The *Palaeomeryx* fold is not found in the sample of large cervids from Perrier-Etouaires. Complete cranial material of *Arvernoceros ardei* is not known. 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.

The some-what larger *Arvernoceros* sp. form Early Pleistocene of Valea Graunceanului (Romania) is represented by fine fragments of antlers and some

cranial remains. The almost complete antler of the deer from Valea Graunceanului (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. 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 (see the antler reconstruction in Croitor 2009: fig. 3D). The general structure of antlers from Valea Graunceanului reminds *Rucervus duvaucelii* (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.

Another long-limbed large (300-400 kg) cursorial form *Arvernoceros giulii* (Kahlke, 1997) is reported from the final Villafranchian of Untermassfeld (Germany). The antler of a young individual from Untermassfeld shows the typical for *Arvernoceros* morphology: the flattened basal tine with an accessory prong is situated at a certain distance from the burr, while the antler beam is terminated with a small bifurcation (Croitor & Kostopoulos 2004). The complete female skull from Untermassfeld figured by Kahlke (2006: p. 24, fig. 9) is characterized by the somewhat elongated facial portion (the anterior edge of orbit is situated above M^3), the relatively small ethmoidal opening with long border with nasale (more than ½ of ethmoidal aperture length), the short nasal bones (the posterior edge of nasals does not reach the anterior orbital line), and clearly expressed preorbital pits. The genus *Arvernoceros* includes also a very large form *Arvernoceros verestchagini* David, 1992 from Villafranchian of Salcia (Moldova), which, however, still maintains a simple plan of antler construction. A similarly giant cervid (the estimated body mass reached 700 kg) from Apollonia (Greece) is characterized by the primitive P_4, the relatively long lower premolar series, the upper molars lacking cingulum, and the conspicuously long metapodials that give to this form of *Arvernoceros* a giraffe-like appearance. The medium-sized species *Axis ubensis* (Vislobokova, 1977) from Pliocene of Altay displays all main characteristics of *Arvernoceros* (a basal tine with accessory prong situated at a certain distance from the burr and a distal small bifurcation). Teilhard de Chardin & Piveteau (1930) described a new species *Cervus (Elaphurus) bifurcatus* from the Early Pleistocene of Nihowan (China) and noticed the affinity of its antlers with *"Cervus" ardeus* from Perrier-Etouaires. Therefore, *Arvernoceros bifurcatus* extends the area of distribution of the genus until Eastern China.

Teilhard de Chardin & Piveteau (1930) supposed that *Cervus ardeus* is closely related to modern *Elaphurus*. Lister (1987) regards *Arvernoceros* as an *incertae sedis* genus. Vislobokova (1990, 2012), following Heintz's (1970) hypothesis on phylogenetic relationship between *Arvernoceros* and *Megaloceros*, 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 based entirely on the plesiomorphic for Cervinae three-pointed structure of antlers shared by *Arvernoceros* and *Axis*, however, this is a simplistic approach, which disregards many others taxonomically meaningful characters provided by cranial and dental morphology. Unlike *Arvernoceros*, *Axis axis* is characterized by relatively short pedicles and has no upper canines. Therefore, *Arvernoceros* is more primitive than *Axis* in this cranial character, but shows more advanced antler morphology. In my previous work (Croitor 2009), I supposed that *Arvernoceros* could be very close to modern *Rucervus* since it shows some apomorphic antler characters seen in modern *Rucervus duvauceli* (the additional prong on basal tine, the posterior insertion of distal crown tines on the antler beam) and shares with the swamp deer the same shape of basioccipitale broadened in pharyngeal tuberosities. However, *Arvernoceros* sp. from Valea Graunceanului shows a doubtless presence of upper canines, which are wanting in *Rucervus duvauceli*. Therefore, the presence of upper canines is a significant character distinguishing *Arvernoceros* from *Rucervus*. However, the upper canines of *Arvernoceros* are a plesiomorphic character and do not exclude the possibility of phyletic relationship between *Arvernoceros* and *Rucervus*. *Arvernoceros* also shows some affinities with *Panolia*, which superficially resembles *Rucervus*, but possess upper canines and phylogenetically is close to *Cervus*. However, *Panolia* and *Cervus* are characterized by narrow basioccipitale, unlike *Rucervus* and *Arvernoceros*. The systematical and diagnostical 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*).

3. 2. 4. Genus *Eucladoceros* Falconer, 1868

Deer of the Villafranchian genus *Eucladoceros* (the estimated body mass varies between 250 and 300 kg) are easily recognizable due to their peculiar
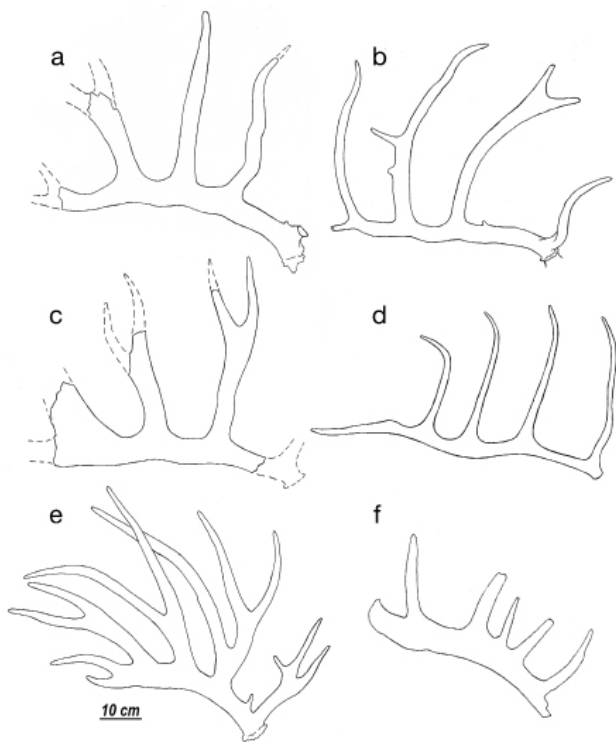
comb-like antlers. Despite of the vast Eurasian area of distribution of *Eucladoceros*, the majority of its species were described in Western Europe. Apparently, only two good species are present in Europe: *Eucladoceros ctenoides* with simple comb-like antlers (Fig. 16 a), and *Eucladoceros dicranios* (the type species) with dichotomously branched tines on its comb-like antlers (Fig. 16 e). *Eucladoceros dicranios* is the most advanced species of the genus, but it still maintains the basic comb-like structure of antlers as can be seen in the species' holotype. The first tine is situated at a certain distance from the burr; an accessory typical for the genus subulate tine is situated in the area of first ramification some-what medially (it is directed upright on the antlered skull); three crown tines inserted on the anterior side of the antler beam. The distal portion of beam is regarded as a "posterior tine" (Azzaroli & Mazza 1992). The antler beam and the tines (with exception of the accessory subulate tine) are pronouncedly compressed from the sides. The antler tines are bifurcated and 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 *Eucladoceros dicranios* represents a sort of hypermorphy, which is strongly expressed in the proximal tines: the first (brow) tine and the first crown tine are 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

Figure 16: Antlers of *Eucladoceros*: **(a)** *Eucladoceros ctenoides ctenoides* (Nesti, 1841) from Upper Valdarno, Italy (IGF377, MGUF); **(b)** *Eucladoceros ctenoides falconeri* (Dawkins, 1868) from Sénèze, 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 Steensma 1988).
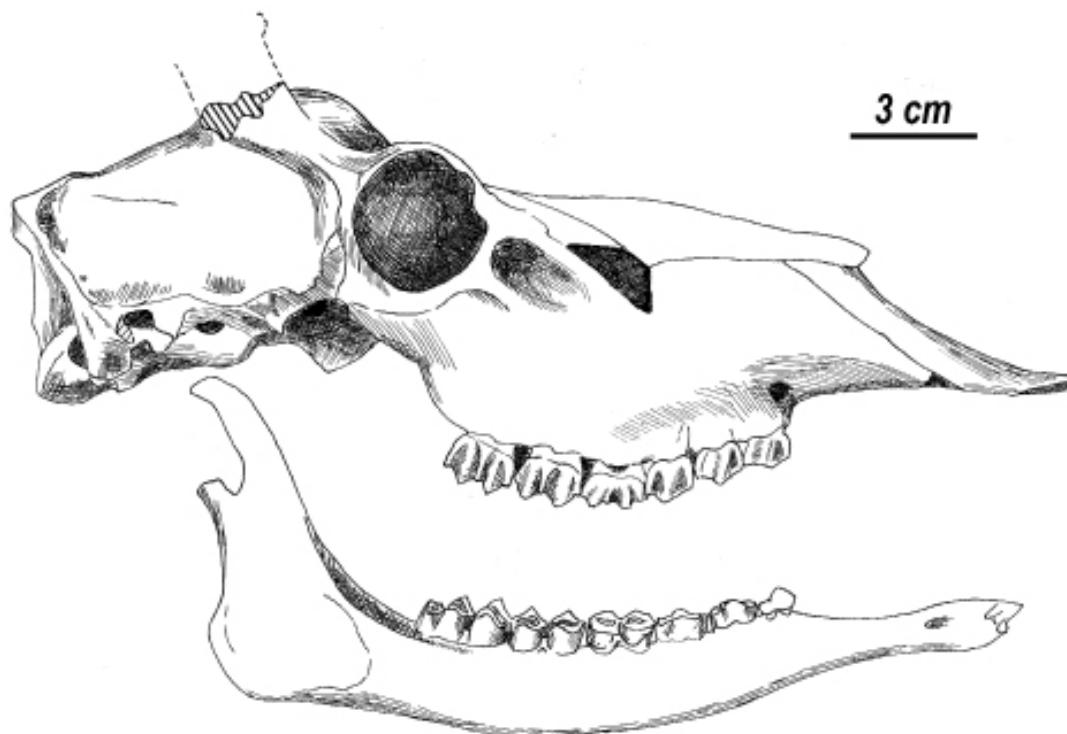

Figure 17: *Eucladoceros ctenoides falconeri* (Dawkins, 1868): the male cranium from Sénèze, France (MNHN).

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 some-what 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. The type specimen comes from Early Pleistocene of Upper Valdarno (Italy). *Eucladoceros dicranios* is quite rare in the paleontological record of Europe. Its known area of distribution ranges from the Azov Sea planes 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. *Eucladoceros sedgwickii* Falconer, 1868 from Bacton, Norfolk (England) is regarded as a junior synonym of *E. dicranios* (Azzaroli 1947; De Vos et al. 1995).

Eucladoceros ctenoides is a less evolved species with simple metameric comb-like antlers possessing four or five tines (the accessory rudimental tine is not counted). The first tine 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. The crown tines are normally compressed from the sides at a variable degree. The crown tines are not reportedly branched. However, it is not unusual when crown tines show a small distal dichotomic ramification in some well-grown hypertrophic specimens. Azzaroli & Mazza (1992) observed that the dichotomous branching is clearly recognizable on the fourth tine of the holotype of *Eucladoceros ctenoides* from Upper Valdarno (Fig. 16 a), even if that tine is not complete. Apparently, the apical fifth tine was also dichotomously branched. A similar spontaneous dichotomy of crown tine is observed in the antlered skulls of *Eucladoceros* from Sénèze (France) (Fig. 16 b) stored in Paris and Basel (Heintz 1970), and some antlers from Olivola (Italy) (Azzaroli 1948). Azzaroli & 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 *Eucladoceros ctenoides* and *Eucladoceros dicranios* and was regarded as a forerunner of those two species. The holotype of *Eucladoceros dicranios olivolanus* is a
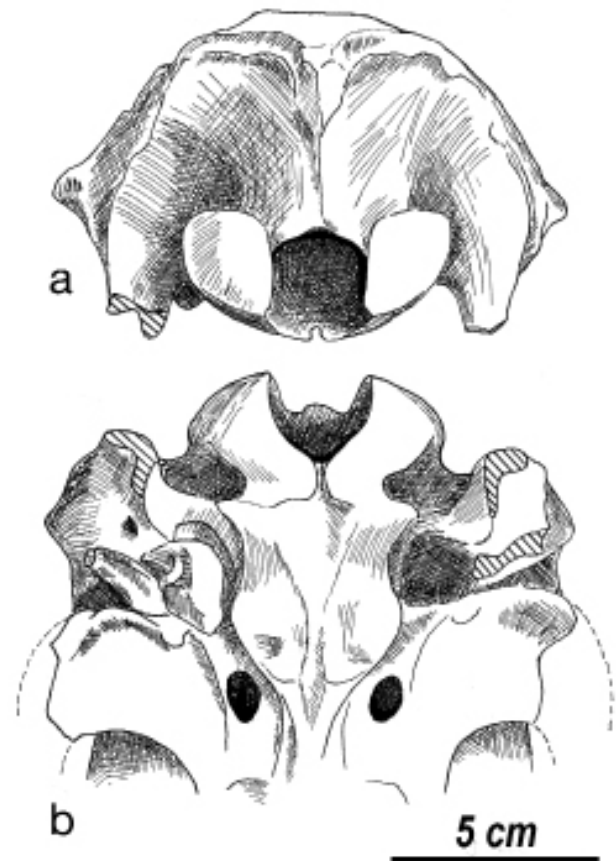

Figure 18: *Eucladoceros ctenoides falconeri* (Dawkins, 1868): the male cranium from Sénèze, France (MNHN) **(a)** occipital view; **(b)** basioccipital view).

distal portion of antler IGF1402 with three crown antlers (Fig. 16 c). Azzaroli (1947) originally described this specimen as *Cervus* (*Euctenoceros*) *ctenoides*. Two crown antlers have their distal parts bifurcated reminding to a certain extent *Eucladoceros dicranios*. The first tine in *Eucladoceros* from Olivola (seen in other specimens) is cylinder-shaped and unbranched as in *Eucladoceros ctenoides*. Since the occasional incipient bifurcation in crown antlers 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 hypermorphy in *Eucladoceros dicranios*, the antler hypertrophy in *Eucladoceros ctenoides ctenoides* is stronger expressed in distal crown tines.

The area of distribution of *Eucladoceros ctenoides* is rather limited and includes only Western and Mediterranean Europe (Croitor & Bonifay 2001). This species is quite polymorphic and is represented by several local and chronological forms distinguished mainly by morphological details of antlers (Azzaroli & Mazza 1992; De Vos et al. 1995). Today, many authors place the numerous species names (*senezen-*

sis, darestei, falconeri, tegulensis, and *tetraceros*) in the list of synonym of *Eucladoceros ctenoides* (De Vos et al. 1995; Pfeiffer 1999; Croitor & Bonifay 2001; Valli & Palombo 2005). Perhaps, some local and chronological variants of *Eucladoceros ctenoides* could be maintained as subspecies: *Eucladoceros ctenoides vireti* Heintz, 1970, *Eucladoceros ctenoides tetraceros* Dawkins, 1878, and *Eucladoceros ctenoides falconeri* (Dawkins, 1868) (= *E. tegulensis* [Dubois, 1904] = *E. darestei* [Deperet, 1931], = *E. senezensis* [Deperet & Mayet, 1910],). *Eucladoceros ctenoides ctenoides* (Fig. 16 a) from Upper Valdarno possess the primary type of antler morphology with respect to more evolved antlers of *Eucladoceros ctenoides falconeri* (Fig. 16 b) with less pronounced metamery, and slim antlers of *Eucladoceros ctenoides tetraceros* (Fig. 16 d), which possibly evolved in the direction of degeneration or under the conditions of starvation. European forms of *Eucladoceros* evolved from Asian immigrant *Eucladoceros* aff. *boulei* (Fig. 16 f) reported from Kapetanios, Greece (Steensma 1988).

Fine cranial remains of *Eucladoceros ctenoides falconeri* are known from Sénèze. One of the skulls (Fig. 17), which was available for this study, is stored in MNHN (no number, exposed in the exhibition). It is characterized by the well-developed preorbital pits, the large ethmoidal openings with very short contact interval with nasals (about 30% of the ethmoidal opening length); the posterior edge of nasal bones almost reaches the line connecting the anterior edges of orbits; bulla tympani are small, oval, with a longitudinal ridge. Basioccipitale is broad, bell-shaped, widened in pharyngeal tuberosities (Fig. 18). The dentition generally is primitive: P_4 normally is not molarized, lower premolar series is moderately short (premolar/molar ratio varies between 55% and 67%), the *Palaeomeryx* fold in lower molars is not present; the upper molars occasionally are supplemented with small protoconal fold and hypoconal spur, entostylids are small. Upper canines are not present. The possible phylogenetical relationships of *Eucladoceros* with modern cervids were not discussed before. The antler morphology of *Eucladoceros ctenoides* reminds to a certain extent modern *Przewalskium albirostris* (I prefer to keep the original spelling of this species name; but see Leslie 2010). However, unlike *Eucladoceros, Przewalskium* possess upper canines (Flerov 1952; Leslie 2010). Therefore, *Eucladoceros* most likely does not belong to the lineage *Przewalskium-Rusa-Cervus* and the similarity in antler shape is superficial.

3. 2. 5. Genus *Praemegaceros* Portis, 1920

The genus includes several Early and Middle Pleistocene continental giant forms with estimated body mass ranging between 300 and 500 kg (*Praemegaceros obscurus* [Azzaroli, 1952], *Praemegaceros pliotarandoides* [De Alessandri, 1903], *Praemegaceros verticornis* [Dawkins, 1852], *Praemegaceros solilhacus* [Robert, 1830]) and two dwarfed survivors: the Middle Pleistocene *Praemegaceros dawkinsi* (Newton, 1892) from England and Northern France (=*Cervus belgrandi* Belgrand, 1869 *nomen oblitum*), and Late Pleistocene *Praemegaceros cazioti* (Deperet, 1897 from Mediterranean islands Corsica and Sardinia. Azzaroli (1979) and Azzaroli & Mazza (1993) included *Praemegaceros* in *Megaceroides* Joleaud, 1914, however *Megaceroides algericus* from North Africa is too aberrant and specialized and can not typify the species of the genus *Praemegaceros* (Croitor 2006b). The main problem of the genus *Praemegaceros* is that its type species *Praemegaceros dawkinsi* is also quite specialized and deviant form characterized by stunted body size, reduced size of palmed antlers with vestigial basal tines, and rather high-crowned cheek teeth (Azzaroli 1953), however its direct phylogenetic relationship with Middle Pleistocene *Praemegaceros obscurus* is obvious (Croitor 2006b). Azzaroli & Mazza (1993) reasonably suggest *Eucladoceros* as a forerunner for *Praemegaceros*, seeking the support for this hypothesis in the analogous general construction of antlers. Unlike *Eucladoceros, Praemegaceros* lost the metameric pattern of distal part of their antlers. Complete skulls are known only for *Praemegaceros obscurus* and *Praemegaceros cazioti*. The cranial morphology of *Praemegaceros obscurus* from the Early Pleistocene site of Pietrafitta (Italy) (= *Megaceroides boldrinii* Azzaroli & Mazza, 1992) reminds *Eucladoceros*: the condylobasal length of skull is 470 mm (measured on the cast IGF4024 stored in Florence); 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), 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, some-what compressed mediolaterally (DAP×DLM = 53.6 mm × 42.5 mm, *dx*); upper canines are missing; P_4 is molarized. Complete fully grown antlers of *Praemegaceros obscurus* are not known, however the available characters of antler morphology are rather specific: the strong basal tine is resting on the burr, the second tine is inserted some-what medially on the beam, is very strong, long, flattened, and bent toward the lateral side of the beam. According to Azzaroli & Mazza (1993), the second tine is an analogue of the accessory prong situated near the basal ramification in *Eucladoceros*. The advanced Middle and Late Pleistocene species of *Praemegaceros* are characterized by significant antero-posterior compression of pedicles and their stronger divergence, the basal tines are reduced, some-times represented by vestigial rudiments or completely vanishing, while their distal parts are expanded into variously shaped palmations (Azzaroli 1979; Croitor 2006b). The general plane of antler morphology,

as well as the variable vestigial remnants of basal tines permitted to distinguish three evolutionary lineages that could have a formal status of subgenera: the subgenus *Praemegaceros* with *Praemegaceros obscurus* – "*Praemegaceros mosbachensis*" (Soergel, 1927) (an advanced form of *obscurus*, the taxonomic status of this form is not clear yet) – *Praemegaceros dawkinsi*; the subgenus *Orthogonoceros* Kahlke, 1956 with *Praemegaceros pliotarandoides* – *Praemegaceros verticornis*; and the subgenus *Nesoleipoceros* Radulesco & Samson, 1967 with two sister species *Praemegaceros solilhacus* and *Praemegaceros cazioti* (Croitor 2006b). Vislobokova (2012) agrees that the antler morphology of the mainland giant *Praemegaceros solilhacus* and the insular dwarfed *Praemegaceros cazioti* is very similar; however she questions the close phylogenetical relationship between these species because of some differences in cranial morphology, without, however, specifying which differences she found. Actually, complete skulls of *Praemegaceros solilhacus* are unknown. It is not clear how closely related the above mentioned lineages and I do not exclude that the genus *Praemegaceros* could be paraphyletic. I agree with Vislobokova (2012) that it seems that the palmations of *Praemegaceros solilhacus* and *Praemegaceros cazioti* derived from posterior tines. The complicated posterior crown tines are known not only in *Dama*, as noticed Vislobokova (2012), but in *Rucervus* too. However, for this moment there are no clear evidences on phylogenetic relationship between *Praemegaceros* (*Nesoleipoceros*) and *Rucervus*.

3. 2. 6. Genus *Praedama* Portis, 1920

The genus contains, most probably, only one Middle Pleistocene (0.8-0.4 Ma) species *Praedama savini* (Dawkins, 1887) (=*Dolichodoryceros suessenbornensis* Kahlke, 1955) with the estimated body size ca. 220 kg (Brugal & Croitor 2007). The species is known only in Europe. The available data on this cervid are incomplete, despite of the fine antlered frontlet found in Suessenborn, Germany (Kahlke 1969). Antlers are characterized by flattened proximal part of basal tine (complete basal tine is not known) situated at a certain distance from burr, a middle tine, a posterior tine and normally three long crown tines, two of which compose a terminal bifurcation of the antler (Kahlke 1969: tab. XXXIV). The antler base is characterized by a specific quadrangular cross-section, while the whole antler is compressed from the sides as in *Eucladoceros*. Reliable findings of dentition and complete skulls are unknown. Azzaroli (1953) regarded the flattened basal tine of antler as an argument for the phyletic relationship between *Praedama savini* and *Megaloceros giganteus*. This point of view was uncritically accepted by other authors (Lister 1987, 1994; Vislobokova 1990, 2012; van der Made & Tong 2008). However, the position of basal

tine high above the burr and the quadrangular shape of antler base in *Praedama savini* are different from the morphological condition seen in *Megaloceros giganteus*, therefore some more strong evidences are needed to reveal the phylogenetic relationship of this little known deer. Some of variants of antlers of *Praedama*, as well as the general compression of antlers and the dichotomous pattern of crown antlers bifurcation rather remind the comb-like dichotomously branched antlers of *Eucladoceros ctenoides*.

3. 2. 7. Genus *Cervus* Linnaeus, 1758

Cervus is the most successful modern cervid genus with an extremely vast circumboreal Palaearctic and Nearctic distribution. Nonetheless, *Cervus* maintains the most primitive plesiomorphic cranial morphology among all cervid genera from the temperate climate latitudes. The well known red deer *Cervus elaphus* is characterized by the comparatively little flexed braincase (less than in *Dama*), the relatively longer pedicles (L=D), which are somewhat divergent and inclined toward the posterior, 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 posterior edge of M^3. 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. P$_4$ normally is molarized. The lower premolar series is quite long and the premolar/molar ratio varies between 60.3% and 65.2% (according to the sample of red deer skulls stored in NMNH of Paris).

The genus *Cervus* appears for the first time in the paleontological record of Western Eurasia in Early Pleistocene. *Cervus nestii* (Azzaroli, 1947) from Late Villafranchian of Tuscany (Italy) is the earliest known and the smallest (the estimated body mass is about 70 kg) true representative of the genus *Cervus*. Azzaroli (1947) described this rather small-sized cervid with primitive four-pointed antlers as *Dama nestii nestii*. Later, Azzaroli (1992) created a new genus *Pseudodama* for the so-called "*Dama*-like" deer with type species *Dama nestii nestii* Azzaroli, 1947 in order to solve the taxonomic uncertainty of several small-sized cervid forms from Early Pleistocene. Azzaroli (1992) attributed also to *Pseudodama* the species *Cervus pardinensis*, *Cervus rhenanus* (= *Cervus philisi*), *Cervus perolensis* and two new species: *Pseudodama lyra* Azzaroli, 1992 and *Pseudodama farnetensis* Azzaroli, 1992. The problem of the genus *Pseudodama* caused controversial opinions in the literature, however many authors agreed that *Pseudodama* is a polyphyletic taxon (De Vos et al.
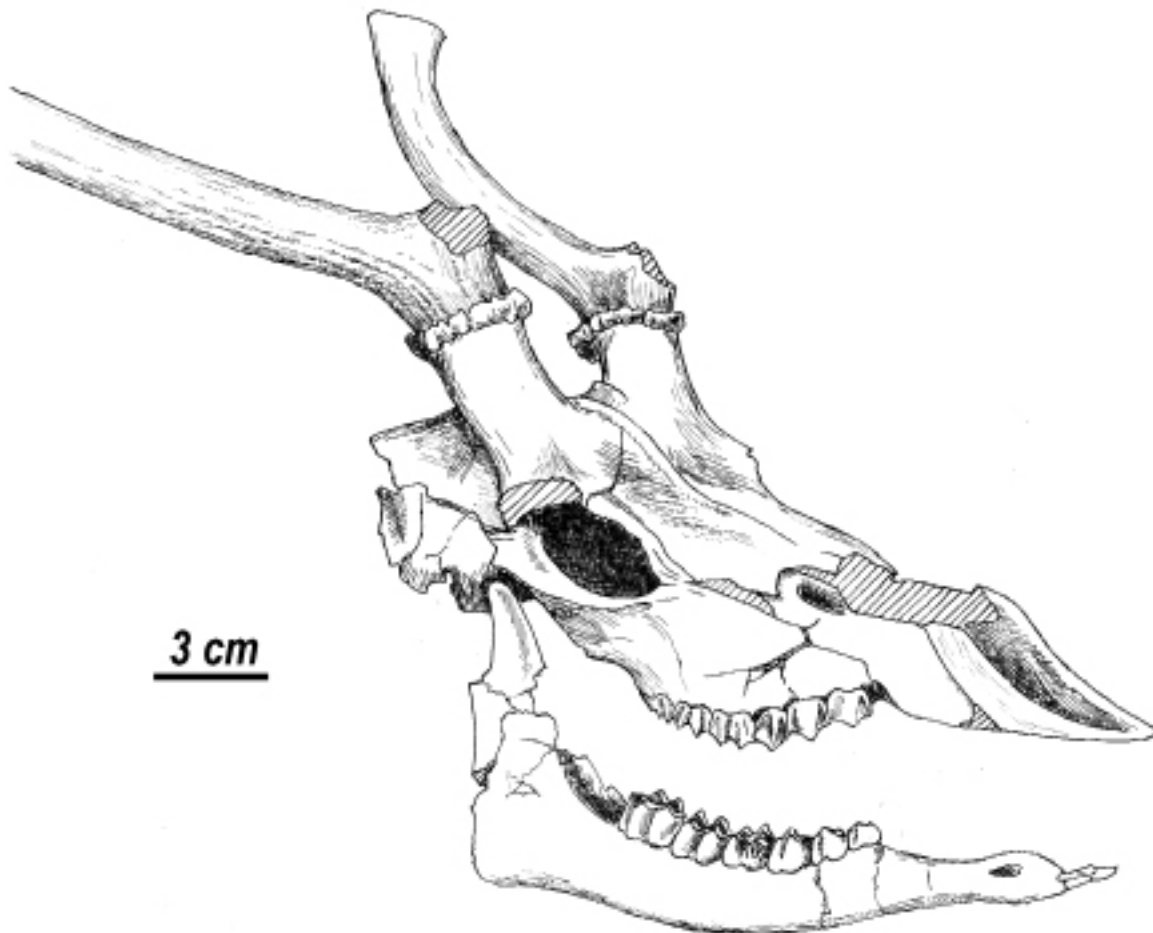
Figure 19: *Cervus nestii* (Azzaroli, 1947): the male skull IGF243 (MGUF) from Figline, Italy.

1995; Croitor 2001b, 2006a, 2012; di Stefano & Petronio 2002). Cranial and dental morphology involved in the study proves that some of species included in *Pseudodama* re-present primitive members of modern genera *Cervus* and *Dama* (*Cervus nestii* and *Dama eurygonos*), other forms belong to extinct lineages *Metacervocerus* and *Praeelaphus* (*Metacervocerus pardinensis*, *Metacervocerus rhenanus*, and *Praeelaphus lyra*) (Croitor 2001b, 2006a, 2012).

The type specimen IGF 363 (MGUF) from Upper Valdarno is a pair of antlers that belongs to a mature individual (Azzaroli 1992: pl. 4, 1a-b). Azzaroli (2001) suggested that the type specimen of *Cervus nestii* is a juvenile individual, however, its pedicles are comparatively short if compared to juvenile specimens from the sample, indicating an adult age (Croitor 2006a). The first tine of right antler and most of the left antler above the basal ramification of the holotype are reconstructed. The tips of the terminal fork of left antler are reconstructed too. The surface of preserved part of antlers does not show clear pearling characteristic of *Cervus elaphus*. The antlers of holotype 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 missing. The middle (or 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]), slightly compressed anteroposteriorly and some-what inclined toward posterior. The antlers of *Cervus nestii* remind the most primitive subspecies of modern red deer *Cervus elaphus barbarus* Bennett from North Africa and *C. elaphus corsicanus* Erxleben from Corsica and Sardinia.

The fairly complete but damaged antlered skull of a young adult male IGF 243 of *Cervus nestii* from Figline (Azzaroli 1992: p.16, Pl. 6, fig. 2) looks as a typical red deer. Its parietal bones are rather flattened. The facial portion of skull is relatively long as in modern red deer: the orbitofrontal region of skull is elongated; the projection of the anterior edge of orbit runs down behind M^3; and the posterior edge of nasal bones does not reach the line connecting the anterior edges of orbits (Fig. 19). The nasal bones have a very short contact with ethmoidal openings (shorter than ½ of the ethmoidal opening length). The length of part of skull between P^2 and prosthion is shorter than
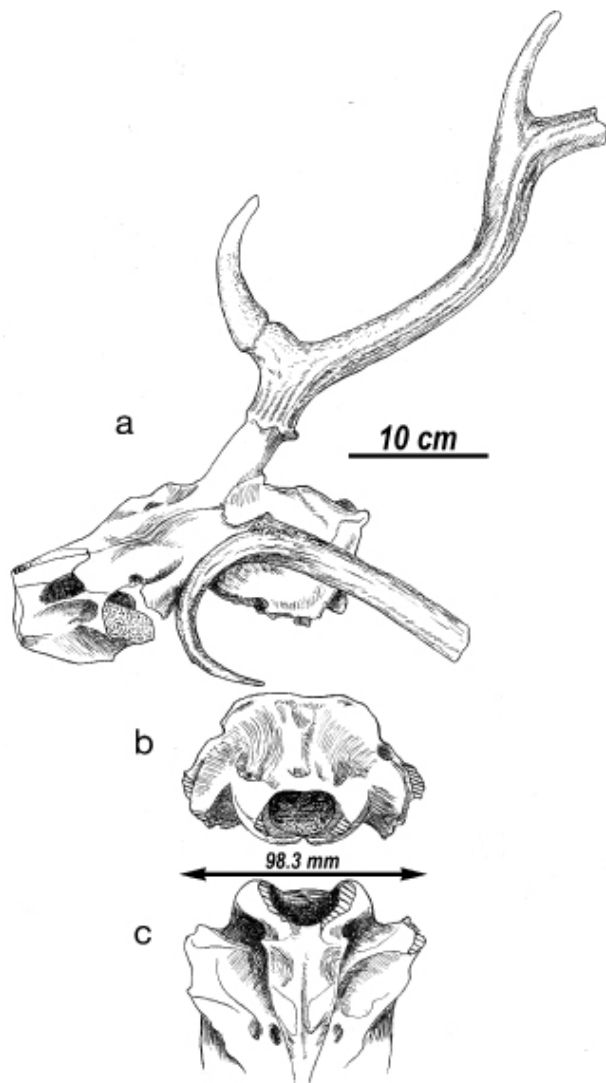
Figure 20: *Cervus nestii* (Azzaroli, 1947): the male skull IGF1403 (MGUF) from Olivola, Italy **(a)**, oblique view; **(b)**, occipital view; **(c)**, basioccipital view). Note narrow triangular basioccipitale.

upper cheek tooth row (see Tab. 1). The preorbital fossae are deep and well developed. The ethmoidal openings are of moderate size. The eye sockets are of moderate size. The facial part measured from the anterior edges of orbits to the anterior tip of premaxillary bones (*prosthion*), is particularly long and consists of 61.2% of the skull length (Croitor 2001b, 2006a). The face of *C. nestii* is relatively longer than in *Dama dama*, *Axis porcinus*, *Cervus nippon* and slightly longer than in *Cervus elaphus corsicanus*. The relative length of face of the specimen under study is close to the modern southern subspecies of red deer *Cervus elaphus bactrianus* and *Cervus elaphus maral*. Pedicels are long and somewhat inclined toward posterior. Frontal bones are flat, slightly depressed between orbits. The lower mandible has a more open angle between horizontal and ascending parts, if compared to *Dama* (this character correlates with elongated orbitofrontal portion of the skull). Upper molars have a small entostyle. The *Palaeomeryx* fold is not present. The morphology of P$_4$ is primitive.

The lower premolar series amounts to 64.3% of the molar series length in the specimen IGF 243. The relative length of lower premolars is similar to modern *Cervus elaphus*. An empty alveolus of upper canine is observed on the right side of the skull. Still older remains of *Cervus nestii* come from Olivola (Tuscany, Italy). The best preserved antlered skull of *Cervus nestii* from Olivola IGF1403 (Fig. 20) is characterized by rather long pedicles (L>D) somewhat inclined toward posterior, the narrow triangular basioccipitale, the pearled surface of antlers as in modern red deer, the first tine situated at a certain distance from the burr (more or less equal to the anteroposterior diameter of the antler base), the circular cross-section of the antler beam. The antler beam is curved toward the posterior in the area of middle (trez) tine. The bez tine is not present. A similar to *Cervus nestii* small-sized deer from Dmanisi (Georgia) is described by Kahlke (2001) as a primitive form of red deer *Cervus abessalomi*. I do not exclude that *Cervus nestii* and *Cervus abessalomi* are synonyms.

The systematical position of *Cervus nestii* is a debated matter. According to Azzaroli (1992), *Pseudodama* is a side phylogenetical branch, which takes its origin from Chinese "*Cervocerus novorossiae*". De Vos et al (1995) preferred to keep *Cervus nestii* in the genus *Pseudodama*, while other small-sized cervids with three-pointed antlers where included in the genus *Cervus*. Pfeiffer (1999) regarded Azzaroli's *Pseudodama* as a subgenus of the genus *Dama*, taking in consideration mostly the morphology of postcranial bones and ignoring the available cranial material. Di Stefano & Petronio (2002) included *Cervus nestii* in the modern genus *Axis*, which, according to the cited authors, is characterized by relatively short splanchnocranium, the longer slender antlers, and the terminal fork oriented in the parasagittal plane. The observations of di Stefano & Petronio (2002) disagree with my conclusions based on the material from Upper Valdarno, in particular, on the skull from Figline (Croitor 2006a). Most probably, di Stefano & Petronio's (2002) conclusions are based on a wrongly determined cranial material. Unlike modern *Axis axis* (the type species of the genus), *Cervus nestii* possesses small upper canines and narrow triangular basioccipitale (Fig. 20 c). In my opinion, any attempts to create a taxonomic unit for all cervid forms sharing only their "*Dama*-like" body size is quite risky, since there is a high probability that this taxonomic unit is an artificial group containing forms sharing just similar ecological specialization.

The modern larger red deer *Cervus elaphus* appears in Western Eurasia by the beginning of Middle Pleistocene in Soleilhac (France), Tiraspol (Moldova), and Tamani (Southern Russia) (Vereschagin 1957; Croitor et al. 2006). The antlers of the first red deer of modern type *Cervus elaphus acoronatus* Beninde possess the second basal (bez) tine, the middle (trez) tine and a simple transversal distal fork, reminding the primitive modern subspecies *Cervus elaphus*

bactrianus Lydekker, 1900 and *Cervus elaphus yarkandensis* Blanford 1892 from central regions of Asia. The sample of cervid remains from Soleilhac contains typical for red deer proximal fragments of antlers with two basal tines (Abbazzi & Lacombat 2005). The distal fragment of antler Sol-225 from Soleilhac (now is stored in the Prehistorical Museum of Tayac, France) represents a simple fork characteristical of *Cervus elaphus acoronatus*. The mandible 2003-4-420-Sol from Soleilhac was originally described as *Megaceros* (*Megaceroides*) *solilhacus* (= *Praemegaceros solilhacus*) by Azzaroli (1979: pl. 3, fig. 2). Unlike *Praemegaceros*, the mandible 2003-4-420-Sol is characterized by a very long diastema, which attains 82.6 % of the lower tooth row length, approaching the proportions of lower mandible of modern red deer (the ratio of diastema length to lower tooth row length varies between 63.0% and 82.5% in the sample of red deer stored in MNHN, n=10). P_4 is not fully molarized: paracone and metacone get in touch, but are not fused. The premolar/molar ratio in the red deer from Soleilhac is typical for this species (60.4%). The primitive shape of P_4 in red deer from Western Europe was recorded until early Late Pleistocene and permitted to Guadelli (1987) to establish the subspecies *Cervus elaphus simplicidens* distinguished by simple P_4. However, this name is already preoccupied by *Cervus simplicidens* Lydekker 1876 from Siwalik Hills.

The opinions on origin of genus *Cervus* and its phylogenetic relationships with fossil forms remain rather speculative. Flerov (1952) assumed that *Cervus elaphus* is related with *Cervavitus* through a range of "transitional" forms like *Cervus* (*Axis*) *pardinensis* Croizet & Jobert and *Cervus* (*Cervus*) *etuerianus* Croizet & Jobert. Janovskaya (1954) described *Cervus* (*Rusa*) *moldavicus* from Pliocene of Moldova and regarded her new species as a transitional form between *Cervavitus* and modern *Cervus elaphus*. A revision of Janovskaya's (1954) species revealed the wrong reconstruction of holotype skull what superficially resembled red deer with elongated splanchnocranium (Croitor 1999). The so-called "Moldavian sambar deer" is a primitive Capreolinae deer, which is included today in the genus *Procapreolus*. According to Vislobokova (1990), the oldest reliable remains of Cervus belong to *Cervus* (*Rusa*) *warthae* from Pliocene of Poland. According to Vislobokova (1990), *Cervus perrieri* from the Late Pliocene of Western Europe is phylogenetically the nearest form to modern red deer. Di Stefano & Petronio (2002) reasonably seek the origin of *Cervus* in Asia and regard Pliocene *Cervus magnus* Zdansky 1925 as the most ancient representative of the genus. According to di Stefano & Petronio (2002), *Cervus magnus* is a forerunner of three parallel lineages: the lineage of *Cervus elaphus*, the lineage of *Cervus warthae* – *Cervus perrieri* (here included in the genus *Praelaphus*), and the lineage of modern *Rucervus duvauceli* and *Panolia eldi*.

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). However, 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. By the present moment, the majority of researchers agree that the genus *Megaloceros* contains only one species *Megaloceros giganteus* (Vislobokova 1990, 2012, 2013; Azzaroli & Mazza 1993; Croitor 2006b; Croitor & Bonifay 2001), however, some students continue to keep *Praedama savini* (= *P. suessenbornensis*) in *Megaloceros* (van der Made & Tong 2008). Azzaroli (1953) regards *Megaloceros giganteus antecedens* with peculiar *Sinomegaceros*-like antlers as a separate species. For a definite well-founded conclusion on specific status of the *antecedens* form, a detailed comparative study of cranial, postcranial, and dental morphology is needed. Several subspecies of giant deer are recognized mostly from the details of shape of their antlers, such as the bending of antler beam and orientation of distal palmation, the direction and position of crown tines, and the shape and size of basal tine (Vislobokova 2012; Croitor et al. 2014). The basal tine is situated very close to the burr, flattened and normally is bilobed; however, it is broad and plate-shaped in *Megaloceros giganteus antecedens*. The second (middle) tine is situated of the anterior side of the beam and some-times may adjoin the distal palmation (as in *antecedens* and, in the less extent, in *Megaloceros giganteus italiae*). The distal palmed part of antler may have different shape, with crown tines inserted on its anterior side (as in the "typical" form from Ireland), or on its distal edge, as in European continental forms *germaniae*, *italiae*, and *ruffii*, which, according to Vislobokova (2012) are synonymous. The posterior tine is normally present on the opposite from the middle tine side of antler; it adjoins the palmation in *antecedens*. Nonetheless, the subspecies of giant deer are still imperfectly known, since the reported broad variability of postcranial skeleton proportions (van der Made 2006) and of dental proportions and morphology (Croitor 2008) is not associated with antler morphology. Vislobokova (2012) regards the sample from Ireland as the nominotypic subspecies *Megaloceros giganteus giganteus*, however, the dispersal of metacarpal proportions suggest that the sample from Ireland is heterogenous and does not represent a single population (Croitor et al. 2014).

Some differences may be seen in cranial morphology of various specimens of giant deer too; however this question needs a special study using well-dated skull samples associated with antlers and

postcranial bones. Here I will indicate just few observations I made studying the skulls from Ireland (stored in NHML and MNHN) and the skull found in Colentina, Southern Romania (NHMB). The pedicles of mature male skulls from Ireland are robust, diverged and directed caudally. Unlike advanced *Praemegaceros*, the frontal bones are concave before the pedicles. Ethmoidal openings are very small or almost completely closed (most probably, the side effect of cranial pachyostosis). Preorbital pits are very small, may be very shallow or clearly expressed, quite deep. 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. Upper canines are not present. The upper molars are supplemented with a cingulum. The cingulum is rather variable and some-times may be present also in upper premolars and even in lower molars. The horizontal ramus of mandible is more or less thick, showing a various degree of pachyostosis. According to Lister (1994), the mandibular pachyostosis may be a dimorphic character stronger expressed in males. The lower premolar series is rather short: the premolar/molar ratio varies between 53.6% and 61.1%. P_4 is always molarized.

Unlike the sample from Ireland, the skull 11.010/50 from Colentina is characterized by larger preorbital pits, larger foramina ovale, relatively longer upper premolar series, and wanting cingulum in upper molars. The length of upper tooth row amounts to 140.7 mm, the length of upper molars – 80.0 mm, the length of upper premolars – 63.0 mm. The underdeveloped or missing cingulum is described also for the comparatively small-sized form of giant deer from Bisnik (Poland) and the larger form with relatively long premolar series from Duruitoarea Veche and Brinzeni (Moldova), therefore, the cingulum in upper molars is not a constant character for *Megaloceros giganteus* (Croitor et al. 2014).

The systematical position of giant deer was a subject of long lasting debates. Lydekker (1898), for instance, included *Megaloceros giganteus* in the so-called "Damine groupe" and suggested its close relationship to the modern fallow deer. Lönnberg (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 Lönnberg (1906) as arguments for the close phylogenetical relationship between *Megaloceros giganteus* and reindeer *Rangifer tarandus*. However, Lister (1994) noticed that the vomerine septum in giant deer does not completely divide the nasal cavity as in the Capreolinae, but only in its anterodorsal part, as in the Cervinae. Lister (1994) assumes that the

ancestry of *Megaloceros giganteus* may lie close to *Praemegaceros verticornis* or *Praedama savini*, but, as the cited author acknowledges, this relationship has not been demonstrated. Apparently, the more or less completely ossified vomerine septum is a variable character and represents a side effect of cranial pachyostosis (Croitor 2006b). Heintz (1970) suggested that *Megaloceros giganteus* could be the 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 where ascribed to *Arvernoceros ardei*. Vislobokova (1990) accepted Heintz's point of view and assumed the origin of both *Arvernoceros* and *Megaloceros* from the poorly known Late Miocene Asian *Praesinomegaceros asiaticus*. Recently, Vislobokova (2009) described a new species *Praesinomegaceros venustus* from the Late Miocene site Taralyk-Cher, Southern Siberia. This is a fine fossil material including an almost complete antler, upper tooth rows, lower mandibles and limb bones that permitted to Vislobokova (2009) to make the emendation the definition of the genus *Praesinomegaceros* Vislobokova 1983. The eco-morphology of the deer from Taralyk-Cher is very peculiar. *Praesinomegaceros venustus* is a rather small/medium-sized cervine form (the estimated body mass is ca. 100 kg) characterized by primitive dentition (the premolar/molar row ratio amounts to 62-65%; P_4 is not molarized), absence of the *Palaeomeryx* fold, plesiometacarpal limbs, and unusually complicated for such a small cervid antlers. Vislobokova (2009, 2012) also reports a moderate to weak pachyostosis of lower mandible. The short and robust antlers are quite specialized. The large flattened basal tine with accessory prong and the high total number of tines are the most evolved characters. Vislobokova (2009, 2012) regards *Praesinomegaceros venustus* as a transitional form between *Cervavitus* from one side and *Sinomegaceros* with *Arvernoceros* from another side. However, the subtriangular cross-section of proximal part of antler beam of the deer from Taralyk-Cher does not correspond to the cylindric shape of beam in *Arvernoceros*. The distal portion of antler is significantly compressed from the sides and represents a bifurcation, each tine of which in its turn is terminated with a small bifurcation. Therefore, the antler construction plan reminds *Praedama* (as suggests Vislobokova 2009) and *Eucladoceros*. The presence of small additional prongs in the area of basal ramification also gives a significant resemblance to *Eucladoceros*. However, unlike *Eucladoceros*, the lingual wall of P^3 is cleft (a sort of "molarization" of upper premolars), while the additional protoconal enamel fold, which is very frequent in European *Eucladoceros*, is not present in the specimens from Taralyk-Cher. It is difficult to find the exact phylogenetic position for *Praesinomegaceros venustus*. This deer is a specialized representative of early radiation of Cervinae

and possibly it belongs to the phylogenetical stock of *Arvernoceros* and *Rucervus* or it could be an early very specialized outshoot of phylogenetic branch of *Eucladoceros*.

3. 2. 9. Genus *Megaceroides* Joleaud, 1914

The genus contains only one species *Megaceroides algericus* (Lydekker, 1890) from Late Pleistocene – Early Holocene of North Africa. This is a very specialized endemic deer of medium size, slightly larger than modern fallow deer. The shape of its skull is extremely aberrant (Croitor 2006b: p. 94, fig. 2). The breadth of skull attains more than 60% of its condylobasal length. Skull bones, with exception of zygomatic arches, are very thick. The braincase is little flexed; parietal bones are flat. The basioccipitale is broad and bell-shaped. The pedicles are comparatively long (their length approximately equals to their transversal diameter), deflected sideward and some-what backward. The frontal bones are flat and very broad. The nasal bones are long and extend behind the line of anterior edges of orbits. Orbits are comparatively large; their anterior edge is situated above M^2/M^1. The ethmoidal vacuities are completely closed. The preorbital fossae are not developed. Upper canines are missing. The body of lower mandible is very low and thick (Fig. 21). The symphisal portion of lower mandible is high. The diastemal part of mandible is relatively very short. The anterior portion of mandible from M_1 to symphisis has a cylindrical shape. Behind M_1, the mandible became higher and more robust. The maximal thickness of mandible is observed behind M_3, in the area of *musculus masseter* insertion. The transversal section of anterior portion of mandible is circular. Antlers are terminated with a palmation. The proximal part of antler beam has a circular transversal section. The first tine is situated very high from the burr. Cheek teeth are conspicuously small. The size of upper third molar is particularly reduced, therefore M^2 is noticeably larger than M^3. A varying small cingulum is present in upper molars. The hypoconal spur and other enamel folds are not developed on upper molars. P_4 is molarized. The proportions of lower tooth row are characterized by relatively diminished and short M_3 and broad M_2 and M_1. The premolar series is comparatively short, however, a broad variation is observed here. The premolar/molar length ratio is comparatively high and amounts to 60.5% in the mandible FIL166 (MNHN), while in the two specimens from Phacocheres it amounts to 45.0% and 52.9% (Hadjouis 1990).

Azzaroli & Mazza (1992) regarded *Megaceroides algericus* as a stunted endemic descent of European *Praemegaceros verticornis*. Unlike *Praemegaceros*, *Megaceroides* is characterized by relatively longer braincase, less compressed pedicles, cranial and mandibular pachyostosis, long nasal bones that extend behind the line connecting anterior edges of orbits (Croitor 2006b). The relatively long braincase is a primitive character that rules out the phyletical relationship between *Megaceroides* and *Praemegaceros*. *Megaceroides* shares with *Megaloceros* the pachyostosis of cranial bones and mandible, little flexed braincase, shape and position of pedicles, the caudally extended nasal bones, and moderate size of bullae tympani. Apparently, *Megaloceros* and *Megaceroides* are two sister lineages sharing such a peculiar apomorphy as the cranial pachyostosis. The striking contrast between strong cranial and mandibular pachyostosis and weak dentition of *Megaceroides algericus* could be explained by its specific ecological niche: the life near water bodies. Perhaps, *Megaceroides algericus* was specialized to forage on soft water vegetation that caused the reduction of cheek tooth size and especially the size of upper and lower third molars and premolars. The exceptionally thick cranial bones represent a sort of helmet, which, apparently, could have a function of the passive defense against predators (for instance, crocodiles) waiting their prey near the water shore.
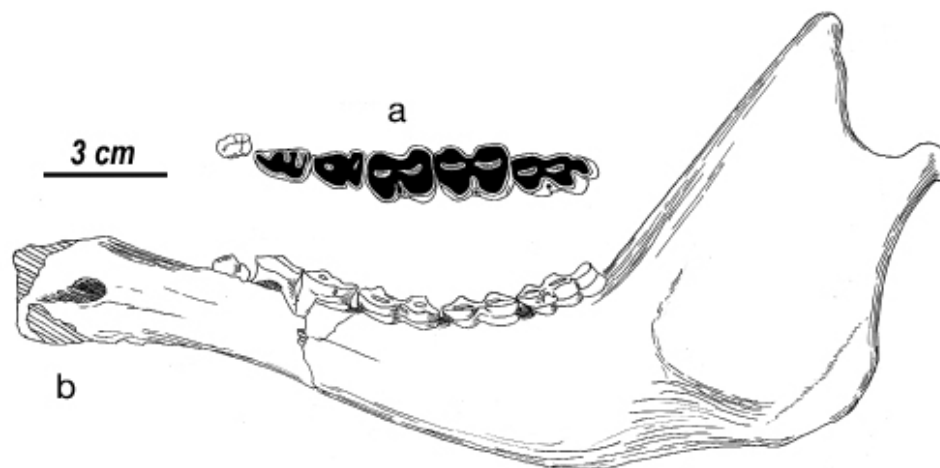

Figure 21: *Megaceroides algericus* (Lydekker, 1890): the lower mandible FIL166 (MNHN) from Filfila, Alger **(a)**, occlusion view of lower tooth row; **(b)**, side view of mandible).
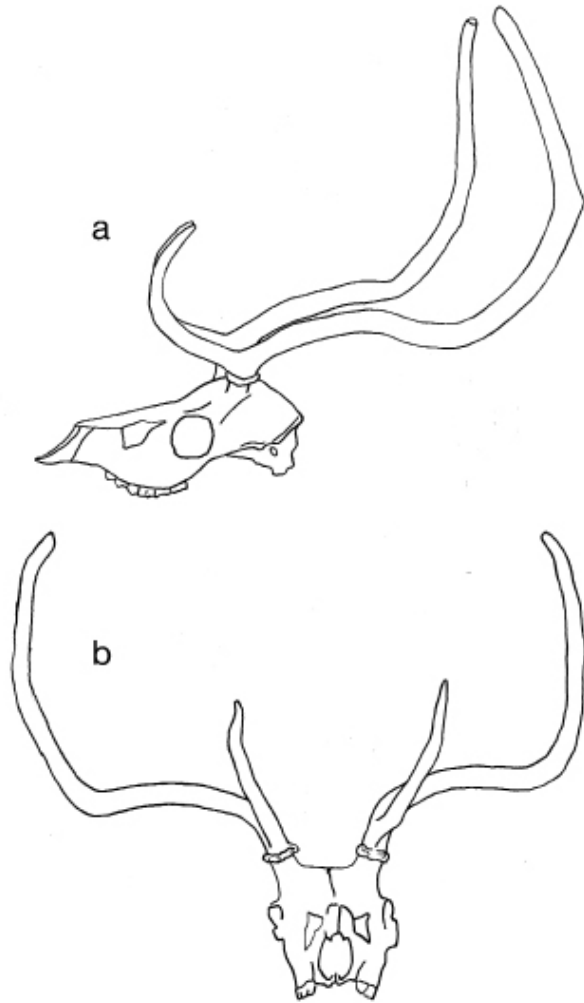
3. 2. 10. Genus *Dama* Frisch, 1775

Figure 22: *Dama vallonnetensis* (De Lumley et al., 1988): the antlered male skull PN-1 (MGUF) from Pirro Nord, Italy **(a)**, side view; **(b)**, frontal view) (adapted from Colucci 1993).

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 incranial (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 nasal bones are extended behind the line connecting anterior edges of orbits; the ethmoidal openings are very large and bordered by nasal bones on more than ½ of their length; the upper canines are wanting, P_4 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*; however, this statement is questionable. *Dama* is more advanced than *Rucervus* in flexed braincase, short nasopraemaxillary articulation, long extended backward nasal bones, and short incranial pedicles. Antlers of *Dama* with crown tines inserted on the posterior side of the beam resemble the structure of antlers of *Rucervus* (most probably, a superficial resemblance), however they are more advanced too. In *Dama*, the simple basal tine is situated at a short distance from the burr. The second (middle) tine is inserted on the anterior side of the beam (it is never present in *Rucervus*). The most remarkable feature
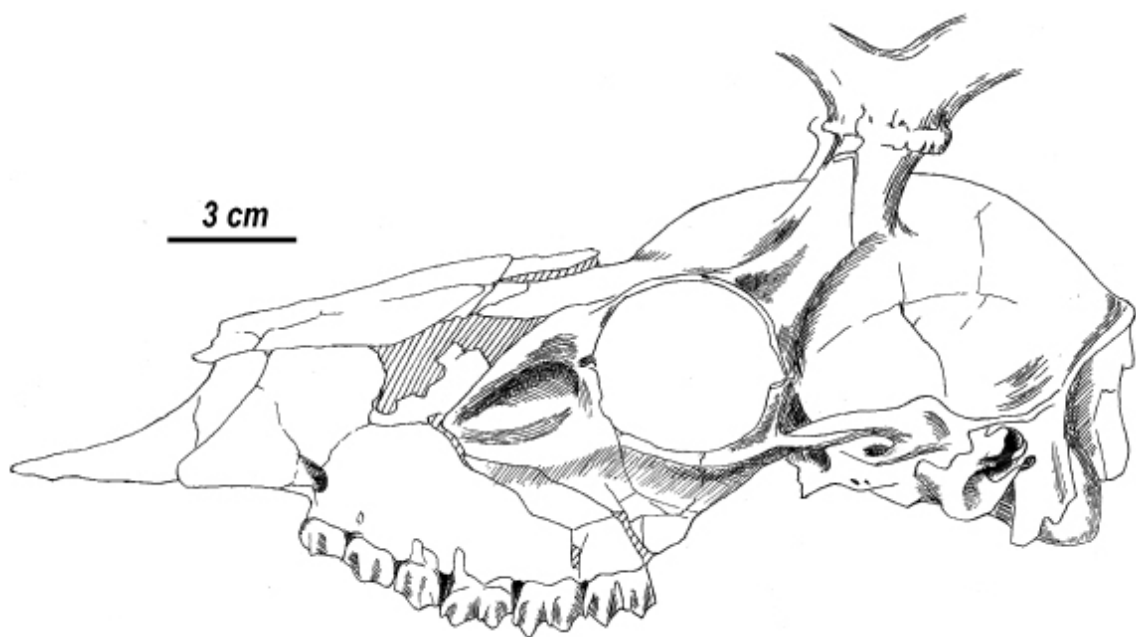

3 cm

Figure 23: *Dama vallonnetensis* (De Lumley et al., 1988): the antlered male skull PN-1 (MGUF) from Pirro Nord, Italy.
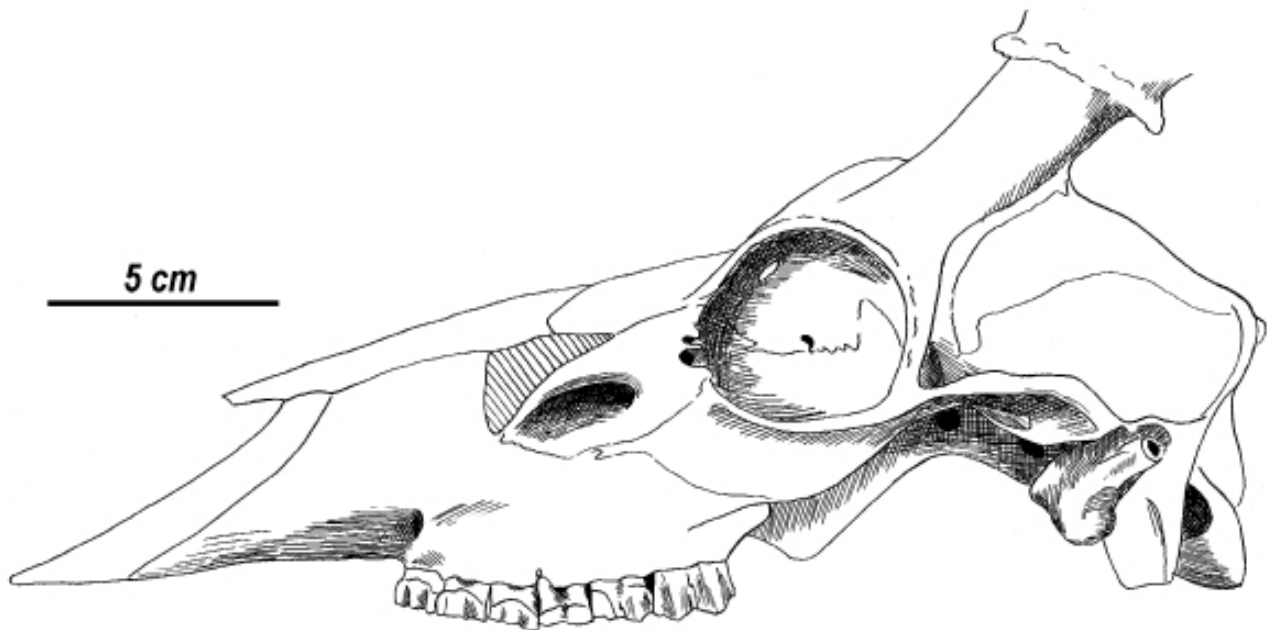
Figure 24: *Axis axis* (Erxleben, 1777): male skull Nr. 12089 ("La Specola", Florence).

of antlers is a palmation that is formed by a series of merged crown tines situated on the posterior side of distal portion of beam. The modern species of the genus are known from Near East (*Dama mesopotamica*) and Northern Mediterranean area (*Dama dama*). All fossil species are known only from Europe and Near East.

The earliest known representative of the genus *Dama eurygonos* Azzaroli 1947 (the estimated body mass amounts to 70-80 kg) from Upper Valdarno (Italy) already shows typical for the genus cranial morphology that can be observed on the skull specimen IGF 244 (NHMF) from Tasso: the flexed, short and domed braincase, the convex frontal and parietal bones, the short pedicles (even in young individuals) in vertical position, the relatively large orbits, the orbitofrontal portion of skull is short (the anterior edge of orbit reaches the level of M^2), the ethmoidal openings are large (Croitor 2006a). Unlike modern *Dama dama*, the posterior edge of nasal bones does not reach behind the line connecting the anterior edges of eye sockets. The preorbital fossae are very large and deep with sharply outlined edges. The ascending part of mandible IGF 242 (NHMF) from Figline has more vertical position if compared to *Cervus*. Antlers of *Dama eurygonos* are simple four-pointed, as one can see on the holotype specimen IGF 245 (Azzaroli 1992: pl. 5, 1a-b). The first tine is strong and branches off at a very open angle close to the burr. The second (trez) tine is small and may be missing in younger individuals (Croitor 2006a). The first and second segments of antler beam are almost of equal length, so the second tine is in more proximal position if compared to *Cervus nestii*. Two massive long tines compose the terminal bifurcation situated in the parasagittal plane. The anterior tine is longer and forms a continuation of the beam, while the second tine is implanted on the posterior side of the beam.

A perfectly preserved cranial material of Early Pleistocene fallow deer is found in the Late Villafranchian site of Pirro Nord (South Italy). The small sized deer from Pirro Nord was reported as *Axis* sp. by Pfeiffer (1999) and *Axis eurygonos* by Petronio et al. (2013). However, the cranial morphology (Figs 22, 23) of the small cervid from Pirro Nord is typical for the genus *Dama*: bullae tympani are very large and inflated as in *Dama dama*, not small and compressed from the sides as in *Axis axis*, the angle between neurocranium and splanchnocranium as in modern *Dama*, the ethmoidal openings have a broad contact with nasale, as in modern *Dama*, not short as in *Axis*. Some measurements of the cranial material from Pirro Nord are quoted in Tab. 1. Just a fleeting glance on cranial shape of the deer from Pirro Nord, modern *Dama dama*, and *Axis axis* (Fig. 24) give a correct conclusion on systematic position of the deer from Pirro Nord. The cervid from Pirro Nord is characterized by advanced molarization of P_4 and relatively short premolar series (premolar/molar ratio varies between 55.3 % and 57.7 %, n=3). Unlike modern fallow deer, the deer from Pirro Nord is characterized by short nasal bones, which are not extended behind the line connecting the anterior edges of orbits, and very broad and massive praemaxillary bones. The antlers of the fallow deer from Pirro Nord are characterized by obtuse first ramification situated very close to the burr, vestigial posterior crown tine represented only by a little knob, and missing middle tine (Fig. 22). The described individual of fallow deer from Pirro Nord is a young male, which, apparently, is very close to *Dama vallonnetensis* (De Lumley et al. 1988) from Capena and Vallonnet. *Dama vallonnetensis* is the latest representative of the lineage of Early Pleistocene fallow deer possessing simplified

Table 1: The measurements of antlered crania of small-sized cervids from Western Europe (sin/dx): *Praeelaphus lyra* (holotype IGF1933v, Ponte a Elsa, MGUF), *Praeelaphus* cf. *lyra* (IGF1378, Olivola, MGUF); *Cervus nestii* (IGF 243, Figline; IGF1403, Olivola, MGUF), *Dama eurygonos* (IGF13962, Petrignano, MGUF); *Dama vallonnetensis* (P.N., Pirro Nord, MGUF).

Measurements	IGF1933v	IGF1378	IGF243	IGF1403	IGF13962	P.N. 1	P.N. 2
CBL			250.0			265.0	
L P²–M³			80.3			84.0	83.0
L M¹–M³			48.1			50.5	50.2
L P²–P⁴			36.0			36.0	35.2
L P²–Pr			74.6			35.7	
L Or–Pr			153.0			148.0	
D above Or							
D of forehead	108.0		92.9	102.3	108.9	88.7	
L Na–Br				82.8		80.5	83.0
D behind Pd		82.0	79.3		83.2		
L Br–Op		76.0	76.0	80.0	74.0	83.2	84.8
L Bs–Op		64.5		60.2	66.6	57.7	
D occipital condyles		58.5		58.5	60.7	53.3	
D occiput				98.1	106.7	88.9	
D Bs		33.5	37.0	38.4	41.4	38.8	38.2
H Pd	27.4/25.0	23.5/--	24.0/20.3		--/20.0		
DAP of Pd	24.7/25.7	32.7/--	25.2/28.4		--/38.7		
DLM of Pd	30.0/29.7	37.3/--	28.6/29.8		--/40.4		
DAP above burr	34.0/35.3	39.8/--		--/39.4			
DLM above burr	33.4/32.1	40.7/--		--/36.6			
H of ramification I	65.8/61.7	69.5/--	43.5	--/53.0			
L between ramifications I and II	480.0/455.0	420.0/--	205.0	--/295.0			

three-pointed antlers with the massive basal tine and the missing middle tine even in fully grown antlers (Croitor 2006a).

The larger Middle Pleistocene *Dama clactoniana* (estimated body mass ca. 140 kg) from Western Europe is the first species of the genus with palmed antlers. Besides the distal palmation, the antlers of *Dama clactoniana* were advanced in presence of multiple crown tines inserted on the anterior and the posterior sides of the palmation axe, unlike modern *Dama dama* (Leonardi & Petronio 1976). This deer is characterized also by relatively longer face and metapodials and apparently was a cursorial species (Croitor 2001b). As I could see on the partially preserved skull from Swanscomb (NHML, Sw-71), its facial morphology is more 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 *Dama dama*.

Di Stefano (1996) described a new subspecies *Dama clactoniana mugarensis* from the Middle Pleis-

tocene of Tabun E, Near East. The material of this peculiar large-medium sized deer is very fragmentary, but interesting: its antlers are characterized by a strong flattened basal tine with an accessory ramification and a flattened proximal portion of antler beam, strongly reminding the antler shape of *Megaloceros giganteus*. Di Stefano (1996) also reports a comparatively strong development of cingulum in upper molars of the deer from Tabun. Di Stefano (1996) regards the modern Persian fallow deer as a survived subspecies of the ancient fallow deer *Dama clactoniana mesopotamica*. This conclusion is based mostly on the similarity of a variant of antler morphology of *Dama clactoniana* from Edesheim with antlers of modern Persian deer; however, the antler from Edesheim still possesses a significantly longer and stronger basal tine.

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 incranially set pedicles (a typical character of *Dama*) are still too long indicating the young age of the individual. The articulations between cranial bones (Breda & Lister 2013: p. 159, fig. 3) are not obliterated, confirming the young age of the individual. 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: p. 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 any convincing arguments that may change our opinion.

Pfeiffer (1997) included in the genus *Dama* also *Cervus reichenaui* Kahlke 2006 (a substitution for the homonymous *Cervus elaphoides* Kahlke 1960) from the Middle Pleistocene of Mosbach Sands. This is a rather small cervid based on incomplete proximal part of antler with basal (brow) and accessory basal (bez) tines. However, the antler specimen with frontal bone figured by Pfeiffer (1997: p. 36, fig. 2) is characterized by an extremely long pedicle (L=58.0 mm; DAP=32.5 mm), which rules out its belonging to *Dama*. According to the reasonable opinion of Lister (1990), *Cervus elaphoides* Kahlke 1960 is based on young individuals of *Cervus elaphus acoronatus*. The true fallow deer is, however, present in Mosbach. The basal fragment of antler NHM1961/1002 (Pfeiffer 1997: p. 39, fig. 4) characterized by a very obtuse first ramification, a massive basal tine situated very close to the burr, and a short incranial pedicle that is very similar to *Dama vallonnetensis*.

The question of origin of the genus *Dama* remains unclear because of multiple taxonomical confusions and misunderstood fossil cervid remains. Di Stefano & Petronio (2002) consider that *Dama clactoniana* evolved from European forms of *Rusa* ("*Rusa rhenana*", =*Metacervocerus rhenanus*). Since the cranial morphology of *Dama* is more advanced than in *Metacervocerus*, it is difficult to confirm or to reject the idea of di Stefano & Petronio (2002). Even if *Metacervocerus* is a forerunner of *Dama*, it should be an earlier representative of the genus, but not Early Pleistocene *Metacervocerus rhenanus* which coexisted with *Dama eurygonos* and *Dama vallonnetensis*.

3. 3. Cervidae *insertae sedis*

3. 3. 1. Genus (?) *Euprox* Stehlin, 1928

Several Pliocene forms of small-sized cervids with simple two-pointed antlers from Eastern and Mediterranean regions of Europe are reported. The findings of those *Muntiacus*-like cervid forms are very fragmental, poorly preserved and rare. Depending on relative length of pedicle, the remains of Pliocene muntiacines are ascribed to Asian genera *Muntiacus* and *Eostyloceros*. Korotkevich (1965a) described from Early Ruscinian fauna of Kuchurgan (Ukraine) few antlers as a new species "*Muntiacus*" *pliocaenicus*. The rather scanty material with badly worn surface does not provide satisfactory information on morphology. The pedicles are of moderate length, compressed lateromedially, very robust if compared to modern *Muntiacus* (Croitor & Stefaniak 2009). The so-called "frontal bony ridges" mentioned by Korotkevich (1965a, 1970) are rather weak roll-shaped structures and do not correspond to the sharp bony ridges characteristical for the modern representatives of the genus *Muntiacus*. The antlers are two-pointed and characterized by a low position of bifurcation and a rather strong and long anterior tine, unlike the weak anterior tine of *Muntiacus*. One can notice that the Pliocene "muntjac" deer from Ukraine rather reminds Late Miocene *Euprox*. It is important to mention in this context, that the earliest known muntjac species *Muntiacus leilaoensis* from Late Miocene of southwestern China already shows all characters diagnostically important for modern *Muntiacus*: the pedicles are very long and extended on the frontal bones with a sharp frontal bony ridge; the main beam of antler is relatively long, while the anterior tine is very small (Dong et al. 2004). The modern genus of *Muntiacus* from South-East Asia is characterized by comparatively high species diversity, which is combined with stenobionty and low vagility (Geist 1998); therefore, it is very improbable that such an ecologically demanding group of cervids could have a vast continent-wide area of distribution across mountains and the arid Asian heartland. Therefore, the belonging of Pliocene small-sized cervids from Eastern Europe with simple two-pointed antlers to the genus *Euprox* known from Late Miocene of Europe seems to be most plausible.

"*Muntiacus*" *polonicus* Czyżewska, 1968 is another species from Early Pliocene site of Węże (Poland) represented only by lower jaw and isolated teeth and potentially is synonymous with the previous species. The species holotype (Nr. 99-Węże-1, IZW) is a fragment of left ramus of mandible with dp_3 and dp_4 at a middle stage of wear and a molar series with M_3 not fully erupted. The molar size of *Muntiacus polonicus* is quite similar to measurements of modern *Muntiacus reevesi*. The estimated body mass based on the type specimen of *Muntiacus polonicus* is about 18 kg. The molars are supplemented with ectostylids and have no *Palaeomeryx* fold. The absence of the *Palaeomeryx* fold distinguishes the specimen of *Muntiacus polonicus* from the Late Miocene *Euprox*; however, this difference does not exclude the possibility of phylogenetic relationship between the deer from Węże and Late Miocene *Euprox*.

"*Eostyloceros*" *pidoplitschkoi* Korotkevich, 1964 was based on few antlers attached to pedicles. According to Korotkevich (1970), the relatively short pedicle (shorter than the height of antler bifurcation) is a diagnostic character of this cervid. The remains of *Eostyloceros pidoplitschkoi* are characterized by smaller size and low position of antler bifurcation if compared to *Eostyloceros blanvillei* from China (Korotkevich 1970). Croitor & Stefaniak (2009) has already noticed the conspicuous resemblance of the "*Eostyloceros*" from Ukraine with Middle-Late Miocene *Euprox furcatus*, however, its pedicles are significantly shorter, if compared to *Euprox*. This cervid form is more often reported and had a larger Ponto-Mediterranean area of distribution (Croitor & Stefaniak 2009). Possibly, "*Eostyloceros*" *pidoplitschkoi* is just a more advanced ontogenetic stage of "*Muntiacus*" *pliocaenicus* and in this case the latter species name falls in the synonymy of *Euprox pidoplitschkoi* (Korotkevich, 1964).

3. 3. 2. Genus *Croizetoceros* Heintz, 1970

The type species of the genus is *Croizetoceros ramosus* from Pliocene and Early Pleistocene (MN16-18) of Western and Mediterranean Europe (Heintz 1970; Kostopoulos & Athanassiou 2005; Brugal & Croitor 2007). This is a rather small-sized plesiometacarpal deer with large complicated antlers and advanced morphology of dentition (Heintz 1970). The estimated body mass is about 50-55 kg. The antler shape of *Croizetoceros ramosus* is peculiar and does not show any 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, 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 an unusual for the Pliocene Cervinae combination of characters. The 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 skull remains of *Croizetoceros ramosus* are rather scanty and diagnostically important characters that may help to reveal the systematic position are not known. Frontal bones are flattened, the forehead behind orbits is sharply narrowed, the pedicles are rather short (their length does not exceed transversal diameter), divergent, some-what inclined backward, the braincase seems to be relatively longer than in modern *Cervus*. The relative length of the lower premolars is as in *Pliocervus*. A clear fossil evidence of the presence of *Croizetoceros ramosus* in Central and Eastern Europe is missing with the exception of few reports of scanty Early Villafranchian remains, which, apparently, resulted from erroneous determinations (Croitor & Stefaniak 2009). *Croizetoceros ramosus* was abundant in Villafranchian of Western Europe and apparently represented an ecological

counterpart of *Procapreolus moldavicus*, which, in its turn, is not known in Western Europe, but is quite common in Central and South-Eastern Europe. The earliest species *Croizetoceros pyrenaicus* with primitive unmolarized P_4 is reported from the Late Miocene (MN13) of Spain (Morales 1984; Azanza 2000). Dong (1996) describes a new species *Croizetoceros proramosus* from the Early Pliocene of France. There are no remains of *Croizetoceros* or a similar cervid found in Asia. Therefore, one can assume that *Croizetoceros* is an endemic European genus.

4. Discussion

The results of molecular phylogenetic analysis show that the subfamily Cervinae in its traditional understanding (plesiometacarpal "Old World deer" possessing large antlers with three or more tines) is monophyletic that is a quite expected confirmation of the earlier broadly accepted viewpoint (Pitra et al. 2004). It was shown also that the primitive tropical cervids with simple two pointed antlers, which traditionally were included in the 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). However, this general dichotomy of Cervidae is not surprising and was already described by Brooke (1878), who established the division of all cervids into Plesiometacarpalia and Telemetacarpalia and reported a more advanced degree of plesiometacarpality for "primitive" modern *Muntiacus*. Therefore, at least among modern cervids, the plesiometacarpal type of limbs occurred only once.

Most likely, the deer of the subfamily Cervinae reached the stage of three-pointed antlers independently in several lineages. This presumption explains the variety of three-pointed antler construction type, which resulted from evolving of the second tine on the anterior side of beam (*Metacervocerus* and, probably, all Cervinae possessing the middle tine), or on the posterior tine (*Rucervus*). One can not exclude that the origin of each tree-pointed antler type evolved independently in more than one lineage. Therefore, the radiation of Cervinae took place at an earlier evolutionary step of a cervid with two-pointed antlers.

One of the most interesting facts resulting from the obtained by Pitra et al. (2004) and Gilbert et al. (2006) cervid phylogenetic tree is that Cervinae (Muntiacini+Cervini) represent a broad Neogene radiation in the eastern part of the Oriental Zoogeographic province, which remains intact until the present days (Geist 1988). The western part of the Oriental Zooheographic province remained inaccessible for Cervinae until Early Pleistocene, when the Old World deer could overcome the Alpine-Hymalayan Mountain belt, which acted for Cervidae as a limiting

zoogeographic border during the Neogene period (Heintz et al. 1990). "*Cervavus*" *rutmeyeri* Schlosser, 1903 and "*Procapreolus*" *latifrons* Schlosser, 1924 and the holometacarpal "*Cervavitus*" *demissus* Teilhart de Chardin & Trassaert 1937 from Neogene of China and Mongolia are conspicuously different from European *Procapreolus* and *Cervavitus* in more robust antlers with cylindrical (not compressed from the sides) beam and tines, with comparatively low position of the first anterior tine, as well as the always absent *Palaeomeryx* fold in lower molars, also belong to the tropical radiation of the Old World cervids. Therefore, the primitive "*Cervavitus*-like" holometacarpal deer and other similar Neogene cervid forms from China and Mongolia require a revision at the level of genus and subfamily.

The radiation of advanced Cervinae, which colonized the vast areas of Eurasia and reached its western regions, is paleontologically better described and seems generally to be compatible with the molecular phylogeny data. The dispersal of Cervinae into the Palearctic Zoogeographic Province could result from repeated North to South fluctuations of Palearctic/Oriental zoogeographic border in Eastern China, as it was described by Tong (2005) for Pleistocene.

According to Douzery & Randy (1997) the divergences within Cervinae appear to be older events, having occurred from the Miocene/Pliocene (3.3-7.1 Myr within the genus *Cervus*) to the Plio-Pleistocene (0.4-2.5 Myr within *Cervus elaphus*). This statement, generally, is in correspondence with the first arrival of Cervinae (*Metacervocerus pardinensis*, *Praeelaphus warthae/lyra*, *Arvernoceros* cf. *ardei*) during Early Pliocene (MN15) in Eastern Europe (Croitor & Stefaniak 2009). Gilbert et al (2006) confirmed that *Rucervus duvauceli* is grouped with the genus *Axis axis* and represents the earliest radiation of Cervinae as previously was suggested by Pitra et al. (2004). According to Pitra et al. (2004), the split between *Axis axis*, *Rucervus schomburgki*, and *Rucervus duvaucelii* on one hand, and the remaining Cervinae on the other, is situated at the base of the Cervinae phylogeny. Croitor (2009) suggested that *Arvernoceros*, which is recorded among the first Cervinae, which dispersed in Europe, shares with modern *Rucervus* the similar plan of antler construction. The comparatively more primitive cranial morphology of *Arvernoceros* than in modern *Rucervus* does not contradict to the possible phylogenetic link between these two genera. Therefore, the genera *Rucervus, Arvernoceros*, *Axis*, *Praeelaphus*, and *Metacervocerus* represent the first radiation of Cervinae. It is interesting to notice, that the extinct *Arvernoceros* and *Praeelaphus*, which colonized the temperate latitudes of Eurasia, possess more advanced shape of antlers than their modern tropical counterparts *Rucervus* and *Axis*.

The rather early divergence within the genus *Cervus sensu stricto*, as suggested by Douzery & Randy (1997), may be confirmed by the early occurrence of *Cervus nestii* in Olivola and Upper Valdarno (Italy), which is already characterized by typical for modern red deer cranial morphology: the advanced elongated splanchnocranium (especially its orbitofrontal portion) combined with the "*Muntiacus*"-like narrow triangular basioccipitale, short nasals, and little upper canines. The frontal orientation of distal antler fork is also a peculiar character shared by *Cervus nestii* and primitive subspecies of red deer *acoronatus*, *bactrianus*, and *yarkandensis*. The case of modern Barbarian red deer from North Africa is interesting in the contexst of present discussion. The geographically isolated *Cervus elaphus corsicanus/ Cervus elaphus barbarus* is the smallest subspecies of red deer characterized by simple four-tined antlers missing the bez tine and white spots on its back (Flerov, 1952). The absent bez tine is regarded by Pitra et al. (2004) as the secondary loss of tine. Pitra et al. (2004) concluded that the *corsicanus-barbarus* clade of the modern red deer almost certainly represents a distinct species from European *Cervus elaphus* (*Cervus corsicanus* Erxleben, 1777 has the priority). Groves & Grubb (2011) also suggest the North African Barbarian deer as a good candidate for species status. Ludt et al. (2004) supposed that the African and Sardinian red deer were subjected to recent gene drift, which provides an explanation for their high differentiation from the other subgroups. Therefore, Ludt et al. (2004) supposed that the obtained time of divergence (2.2 Ma) of *Cervus elaphus corsicanus* from Eurasian subspecies of *Cervus elaphus* is a possible overestimation. However, *Cervus corsicanus* could be a primitive descent of Early Pleistocene *Cervus nestii*, which survived in the remote North African refugium. In this case, the North African deer deserve a full specific rank as it was suggested earlier by Pitra et al. (2004) and Groves & Grubb (2011), and the early divergence of the North African stag obtained by Ludt et al. (2004) is not an overestimation.

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 Early Pliocene (Pitra et al. 2004), or around 3.0 Ma (Gilbert et al. 2006). This statement is in accordance with first occurrence of Cervinae in Western Eurasia, which, most probably, gave the local radiation of the genus *Dama* and, possibly, some other closely related genera, in Western Europe and Eastern Mediterranean area. The most probable forerunner of *Dama* is Early Pliocene *Metacervocerus pardinensis* from Eastern Europe characterized by simple tree-pointed antlers and strong cingulum in upper molars. The first typical *Dama* (although without characteristic palmation of antlers) appeared in Early Pleistocene Upper Valdarno and Val di Chiana (Italy) (Croitor 2006a). Apparently, the Mediterranean fallow deer changed very little during their presence in the paleontological record for almost 2 million years. The cranial morphology

of *Dama eurygonos* from Upper Valdarno is already advanced and does not show any differences from modern *Dama dama*: the braincase is flexed, with confex parietals, the pedicles are short and incranial, the orbits are relatively large, the ethmoidal vacuieties are comparatively very large. The antlers of *Dama eurygonos* are primitive four-pointed, however, they already show some significant characters for the genus *Dama*: the very obtuse angle of basal tine and the crown tine inserted on posterior side of the antler beam. 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 ca. 400 kyr BP (Lister 1994; Lister et al. 2005), however, the estimated divergence of *Dama* and *Megaloceros* could have occurred very early, ca. 10.7 Myr ago (Hughes et al. 2006), i. e., apparently, well before the forerunner of *Dama* dispersed in Western Eurasia. Unlike *Dama*, *Megaloceros* is characterized by more primitive cranial morphology, expressed in less flexed braincase and non-incranial pedicles. *Megaloceros giganteus* was characterized by vast boreal distribution ranging from Ireland to Central Siberia (Lister et al. 2005); however, the exact area of its origin is unknown. The morphologically nearest to giant deer *Megaceroides algericus* from Late Pleistocene and Holocene of North Africa also comes from the Mediterranean area. Here I would like to draw attention to the little known "*Dama mesopotamica*" *mugarensis* di Stefano 1996 from the Late Middle Pleistocene of Tabun (Middle East). This medium-sized cervid actually strongly reminds *Megaloceros* by its flattened bifurcated basal tine, significantly flattened antler beam, and presence of cingulum in upper molars. The cervid from Tabun appears soon after the dispersal of *Megaloceros* in Europe and, possibly, belongs to *Megaloceros-Megaceroides* stock and is a direct forerunner of *Megaceroides algericus*. *Megaceroides algericus* represents an interesting example of adaptation to an ecological niche (periaquatic or semiaquatic herbivore), where a cervid could avoid the ecological competition with competitively strong African bovides.

The phylogenetic position of *Eucladoceros* among Cervinae is not clear. The cranial morphology, as already it was mentioned above, indicates that *Eucladoceros* most probably does not belong to the established by Pitra et al. (2004) stock of *Cervus* and allied forms (*Przewalskium*, *Rusa*, *Panolia*, and *Hyelaphus*). Dong & Ye (1996) reported the earliest species *Eucladoceros proboulei* from Early Pliocene of Yushe Basin (China). If such an early occurrence of *Eucladoceros* is correct, one can assume that this genus is phylogenetically related to a three-tined primitive forerunner of *Axis*, *Metacervocerus*, or even *Rucervus* type. All these genera share primitive cranial morphology and absence of upper canines.

The complicated antlers of *Eucladoceros* probably derived from the three-pointed antler type with insertion of the second tine on the anterior side of beam through the repeated metameric reproduction of the distal branch. Possibly, *Praesinomegaceros venustus* from Late Miocene of Central Asia is also closely related to *Eucladoceros*.

Unlike Cervinae, the phylogenetical clade of modern Eurasian Capreolinae seems to be significantly depleted, since many of evolutionary branches gone extinct, therefore 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 where stronger affected by climate changes. Despite of previous attempts to find the place of some Late Miocene "crown cervids" (*sensu* Azanza et al. 2013) from Eastern Europe in the phylogenetical clade of the "Old World" deer grouped in the subfamily Cervinae (Flerov 1952; Janovskaya 1954; Vislobokova 1990; di Stefano & Petronio 2002), obviously, all Late Miocene medium-sized cervids from Europe with three and more tines on their antlers represent the early adaptive radiation of the subfamily Capreolinae. Unlike coeval Cervids from the Oriental adaptive radiation coming from Neogene paleontological record of China and Mongolia, 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 praemolar (P_4) has a trend toward early advanced high molarization (*Procapreolus moldavicus*, *Cervavitus variabilis*, *Pavlodaria orlovi*) in combination with such a primitive characteristic as relatively long premolar series. The genus *Alces* perfectly fits to the extrapolation of this evolutionary trend: the lower molars in some species (*Alces gallicus*) still preserve remnants of the *Palaeomeryx* fold, the premolars P_4 and P_3 are highly molarized, while the premolar tooth series remains relatively long. Unlike Cervinae, the antler construction in Capreolinae is rather uniform. The basic tree-pointed "roe deer type" antler plan construction is recognizable in all modern and fossil Capreolinae cervids with large antlers (excluding *Mazama* and *Pudu* with simplified antlers), even in such specialized genus as *Alces*, and suggests that the forerunner of modern radiation of Capreolinae possessed the more advanced antlers with three tines: the high-positioned first anterior tine, and two more or less similar in size tines forming a distal parasagittal fork.

According to Douzery & Randy (1997), the clade of Capreolinae may have occurred between 8.7 and 10.4 Ma. This estimation is close to the stratigraphic distribution of the earliest known capreolines: *Pliocervus matheroni* from Western Europe (MN 12-13, 5.3-8.2 Ma); *Procapreolus ucrainica* from Eastern

Europe (MN11-12, 7.1-9.0 Ma), and *Procapreolus loczii* from Pannonia (MN10, 9.7 Ma) (Valli 2010 and references therein). As Cervinae, the Late Miocene radiation of Capreolinae initially included the whole spectrum of ecological and evolutionary forms that included *Cervavitus* with large palmed antlers and the *Muntiacus*-like *Procapreolus* from Eastern Europe, *Pliocervus* from Western Europe with large upper canines and four-tined antlers, and *Pavlodaria* from Kazakhstan with flattened 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). *Procapreolus* from Western Eurasia represents the primitive type of Capreolinae. The general cervid plesiomorphic characters like long pedicles, large preorbital fossae as in *Muntiacus*, and large upper canines are combined with specific for basal Capreolinae characters as the *Palaeomeryx* fold in lower molars, advanced molarization of P⁴, and tree-tined antlers. Most probably, this is an extinct branch of Capreolinae. The earliest finding of *Capreolus* in Udunga, Trans-Baikal area of Russia (Vislobokova et al. 1995), suggest that the origin of roe deer took place in the eastern part of Palearctic.

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 (Fig. 9), relatively long lower premolar series, advanced molarization of P_4, missing complete separation of choanae, *Palaeomeryx* fold in lower molars. The long horizontal beams of *Alces gallicus* are regarded here as very elongated basal segments of antlers below the first ramification that represent an extreme specialization. The time of divergence of Capreolini+Alceini (7.4 Ma: Gilbert et al. 2006) corresponds to the occurrence of *Cervavitus* in Vallesian-Turolian of Moldova (MN 10-12, 7.1-9.5 Ma) (Petronio et al. 2007; Dong 2011).

It is not clear if the rich variety of Late Miocene endemic cervids from Western Europe (Azanza 2000) and Pliocene survivors *Croizetoceros ramosus* and similar to *Euprox* "*Muntiacus*" *pliocaenicus* and "*Eostyloceros*" *pidoplitschkoi*, belong to the adaptive radiation of Capreolinae or represent their own clade. According to Azanza et al. (2013), the direct precursors of Capreolinae migrated to the Western European zoogeographic realm during Vallesian and Turolian from East and coexisted with local endemic muntjac-like forms.

5. Conclusions

Each of the modern cervid subfamlies Cervinae and Capreolinae resulted from the ancient (Late Miocene) adaptive radiation within zoogeographic provinces: the eastern part of the Oriental province and the Palearctic province correspondingly. Cervinae (Muntiacini+Cervini) represent a broad Neogene adaptive radiation in the eastern part of the Oriental Zoogeographic province, which remains generally intact until the present. The majority of phylogenetical lineages of Cervinae, which extincted during Plio-Pleistocene (*Eucladoceros*, *Praemegaceros*, *Arvernoceros*, *Praeelaphus*, *Megaloceros*, etc.), had temperate and boreal latitude distribution. The tribe Megalocerotini Brookes, 1828 (=Megacerini Viret 1961) is an artificial poly/paraphyletic taxon containing cervines from various phyletical lineages that evolved a specific giant eco-morphological type and therefore should be rejected.

Unlike Cervinae, the phylogenetical clade of modern Eurasian Capreolinae is significantly depleted. *Pliocervus matheronis* from Late Miocene of Mont Luberon (France) is closely related to *Pavlodaria orlovi* (Kazakhstan) and should be placed in Capreolinae. The subfamily Pliocervinae Symeonidis 1974 is synonymous with Capreolinae Brookes, 1828. Correspondingly, the tribe Pliocervini Symeonidis, 1974 should be included in the subfamily Capreolinae and restricted to the genera *Pliocervus* and *Pavlodaria*. The genus *Cervavitus* should be restricted to the Late Miocene material from Eastern Europe and is regarded here as another primitive genus of Capreolinae. Possibly, *Cervavitus* is closely related to a forerunner of modern *Alces*. *Cervavitus* shares with *Alces* (including *Alces gallicus*) the general plan of antler construction, the relatively long lower premolar series, the advanced molarization of P_4 (in *Cervavitus variabilis*), and the *Palaeomeryx* fold in lower molars. The *Palaeomeryx* fold is a plesiomorphic character of the Capreolinae radiation; therefore, it is a valuable diagnostic character of early forms of Capreolinae. The genus *Procapreolus* according to the understanding proposed by Korotkevich (1970) is a polyphyletic taxon. The European and the Eastern Asian forms should be placed in different genera and, most probably, in subfamilies Capreolinae and Cervinae correspondingly. *Procapreolus* from Late Miocene and Pliocene of Eastern Europe is a primitive extinct lineage of Capreolinae that shares a series of cranial and dental characters with modern *Muntiacus* (large upper canines, long sloped backward pedicles, large preorbital pits) and *Odocoileus* (large distance between pedicles, molarized lower P_4, upper molar morphology), but also retains specific primitive characters like *Palaeomeryx* fold in lower molars.

Possibly, the endemic primitive muntjac-like cervids from Late Miocene of Western Europe and their Pliocene descendants *Croizetoceros ramosus* and similar to *Euprox* "*Muntiacus*" *pliocaenicus/polonicus* and "*Eostyloceros*" *pidoplitschkoi* represent a local adaptive radiation within the Western European paleozoogeographic province. Most probably, *Croi-

zetoceros does not belong to the radiation of Asian Cervinae and evolved its plesiometacarpal limbs independently.

Acknowledgements

6. References

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