

A SKULL OF *PRAEMEGACEROS PLIOTARANDOIDES* (CERVIDAE, MAMMALIA) FROM THE TAMAN PENINSULA (SOUTH-WEST RUSSIA)

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Abstract. The article presents a description of an antlered skull of the large-sized deer *Praemegaceros* (*Orthogonoceros*) *pliotarandoides* (De Alessandri, 1903) stored in the Regional Museum of Krasnodar. The paleobiology of this species, and a hypothesized model of evolution and speciation within the genera *Eucladoceros* and *Praemegaceros* are also discussed. The climate gradient, from strong continental conditions in the Asian heartland to mild climate conditions in Western Europe and Eastern China, in combination with geographical barriers such as Alpine Mountain Chain and Parathetys Basin, are considered to represent the main control factors of speciation in *Eucladoceros* and *Praemegaceros*.

Keywords: *Praemegaceros pliotarandoides*, Cervidae, paleobiology, paleozoogeography, evolution, Plio-Pleistocene, Eurasia.

INTRODUCTION

The large mammals fauna from late Early Pleistocene fossiliferous sites of Taman Peninsula (South Russia) was described by Verestchagin more than half a century ago, in 1957. The fauna generally has a "Post-Villafranchian" character and is characterized by several archaic and endemic forms, such as *Mammuthus meridionalis tamanensis* DUBROVO 1964, *Elasmotherium caucasicum* BORISSJAK 1914, *Eobison tamanensis* (VERESCHAGIN, 1959), *Canis tamanensis* VERESCHAGIN 1957, *C. (Xenocyon) lycaonoides* (KRETZOI, 1938), *Lutra simplicidens tamanensis* SOTNIKOVA 2009, *Pachycrocuta brevirostris* (AUMARD, 1846), and *Homotherium latidens* (OWEN, 1846) (Verestchagin, 1957; Flerov, 1972; Sotnikova & Titov, 2009). The systematic position of the Tamanian deer was neither revised nor studied in detail since Verestchagin's (1957) paper. According to the original description, the Tamanian fauna includes several deer taxa, the majority with unclear systematic position: *Eucladoceros* sp. 1 (large form), *Eucladoceros* sp. 2 (small-sized), *Megaceros* sp., a deer from the so-called "group of *Cervus elaphus*", some antler fragments tentatively ascribed to "*Cervodama pontoborealis*" PIDOPLICHKO & FLEROV, 1952, and a new genus and species based on a very poor frontal fragment with a small piece of antler base, *Tamanalces caucasicus* (VERESTCHAGIN, 1957). In my preliminary study (Croitor, 2005) I suggested the presence of three large-sized species of deer in the composition of the Tamanian fauna: *Praemegaceros pliotarandoides* (DE ALESSANDRI, 1903) (*Eucladoceros* sp. 1 and Cervidae indet. "ex gr. *Cervus elaphus*" fide Vereschagin, 1957); *Praemegaceros obscurus* (Vereschagin's *Megaceros* sp.); and *Praemegaceros solilhacus* (Vereschagin's *Tamanalces caucasicus* and *Cervodama*). *Tamanalces caucasicus* is a junior synonym of *Praemegaceros solilhacus*, while *Cervodama pontoborealis* is described based on an antler rather belonging to the modern *Alces alces* (Croitor, 2006 a, b).

The article presents a morphological description of an unpublished skull of *Praemegaceros pliotarandoides*, which is supposed to come from the classical Tamanian faunal assemblage, as well as proposes a new model of speciation of two closely related genera *Praemegaceros*

and *Eucladoceros* from Northern Eurasia. The new evolutionary model explains the presence in the Tamanian fauna of three species of the genus *Praemegaceros* that represent, actually, the same ecotype: a large-sized open-landscape herbivore with opportunistic feeding habits and capacity to tolerate comparatively high content of cellulose fiber in the forage (Brugal & Croitor, 2007).

MATERIAL AND METHOD

Specimen KM388 is stored in the Krasnodar Regional Museum, Russia. The exact locality where the specimen was discovered is unknown. One can assume that the antlered skull KM388 is part of the sample originating from the Early Pleistocene site of Tzimbak (Taman Peninsula, Russia), which, according to Vereschagin (1957), was transported to the Regional Museum of Krasnodar. The braincase with the left pedicle and the basal portion of the antler is associated with fragments of the right antler. Some parts of the right antler are lost. Dr. V. S. Baigusheva kindly provided a natural size outline drawing of the complete (or reconstructed) antler made by Dr. N. I. Burchak-Abramovich (unpublished). We used this drawing in the reconstruction of the antler presented in Fig. 5.

The terminology of antler morphology used in this study (see Figs. 1 and 5) is adapted from Azzaroli & Mazza (1992a) and Croitor (2006a). The total frontal breadth and the skull breadth above the orbits of the specimen from Krasnodar are calculated from ½ of the measured variable.

The comparative material involved in the present study is stored in the Museum of Geology and Paleontology of the University of Florence: a braincase of *Praemegaceros pliotarandoides* from Borgo Nuovo (IGF3980V, cast) originally described by Azzaroli as *Megaceros verticornis* (Azzaroli, 1976), an antlered skull of *Praemegaceros obscurus* from Pietrafitta (IGF4024, cast) originally described by Azzaroli & Mazza (1992a) as *Megaceroides boldrinii* sp. nov., and an antlered skull of *Eucladoceros dicranios* (IGF270, holotype).

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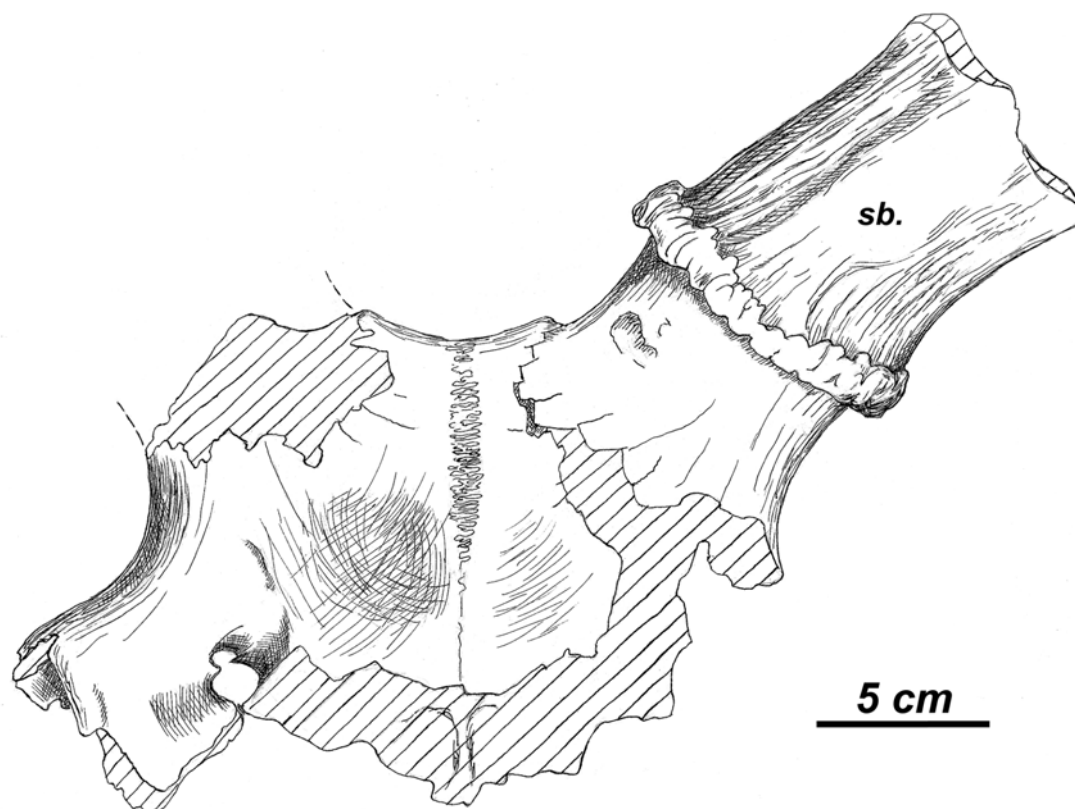


Fig. 1 - *Praemegaceros (Orthogonoceros) pliotarandoides*: frontal view of skull KM388; sb, subbasal tine.

DESCRIPTION

Skull. The skull KM388 belongs to a very large deer. Frontal bones are concave (Figs. 1, 2). The frontal suture is some-what elevated in front of the pedicles, while it is not protruding between the pedicles.

The pedicle is strong and slightly compressed in the antero-posterior direction. The shape of the transversal cross-section of the pedicle is irregular ovoid. Its length is moderate. The pedicle is set on the frontal bone obliquely, deviated slightly toward posterior and sideward directions. The surface of the parietal bones is embossed and sculptured with bony ridges. The basioccipitale is broad and trapezium-shaped, caudally extended (Fig. 3). The *Foramen ovale* is large, irregular and ovoid-shaped (*sin.* 16.0 × 11.3 mm; *dx* 15.7 × 9.6 mm). The occipital surface is supplemented with strong ridges and pits for the attachment of the nugal muscles (Fig. 4). The skull measurements slightly exceed the measurements of *P. pliotarandoides* and *P. obscurus* from Italy, and are significantly larger than *Eucladoceros* (see Tab. 1). The specimen from Krasnodar is characterized by relatively low occiput if compared to the specimen from Borgo Nuovo.

Antler. The antler is broken into four large fragments and very little could be said about its general construction (Fig. 5, Tab. 2). The antler fragment interpreted according to Burchak-Abramovich's reconstruction as a posterior one raises some doubts. Possibly, this piece of antler even does not belong to the individual under study. The largest preserved pieces of antler are the basal portion, with basal tine broken off and preserved part of pedicle, and a distal part of antler, representing two consecutive

dichotomous branching. The burr is well-developed, ring-shaped. A weak button-like vestige of the subbasal tine is visible on the anterior side of the antler base, close to the burr. The outer tine springs off at a certain distance from the burr. It is situated on the antero-medial surface of the beam and its basal portion is directed outward; that is typical for many species of the genus *Praemegaceros* (subgenera *Praemegaceros* and *Orthogonoceros*). The antler beam is curved backward from the basal tine. The lateral side of the antler beam has a longitudinal groove at the level of the first tine. The groove becomes shallower in its distal portion and then disappears. The lateral side of the distal portion of antler beam is quite flat. The distal fragment represents a first dichotomous branching and the next posterior bifurcation that is terminated by two posterior long crown tines (the length of the preserved major part of the third tine is 680 mm). The anterior part of the antler crown with first and second crown tines is not preserved. The antler surface is covered with small and dense longitudinal ridge and furrow ornament. This ornament is some-what broader and undulated above the basal tine.

The diagnostically meaningful characters that confirm the determination of the skull from Krasnodar to *Praemegaceros pliotarandoides* are the following: the cylindrical shape of the pedicle, which is just slightly antero-posteriorly compressed; the vestigial button-like subbasal tine; the presence of the outer tine, situated on the antero-medial side of the antler beam and directed outwards; and the lack of middle tine (Croitor, 2006a).

Measurements (mm)	KM388	IGF3980V	IGF4024	IGF270
Length of basioccipitale	136.0		123.0	
Occipital breadth	172.6	164.4		150.0
Breadth of occipital condyles	93.0	90.3		77.9
Occipital height from foramen magnum	75.0	79.3		62.5
Occipital height from basioccipitale	110.0	112.0		90.9
½ breadth above eye sockets	101.0			160.7
Frontal breadth	170.0	163.6		149.1
Braincase breadth behind pedicles	127.4	120.8		109.2
Maximal breadth of basioccipitale	70.0	64.6	61.5	58.0
Basioccipital breadth at pharyngeal tuberosities	53.0			
Distance from orbit to occiput	143.8		140.0	131.8
Distance from bregma point to occiput	101.5	86.2		92.5

Table 1 - Measurements of the skull of *Praemegaceros pliotarandoides* stored in the Regional Museum of Krasnodar (KM388, Russia) compared to measurements of *P. pliotarandoides* from Borgo Nuovo (IGF3980V, Italy), *P. obscurus* from Pietrafitta (IGF4024, Italy), and *Eucladoceros dicranios* from Upper Valdarno (IGF270, Italy).

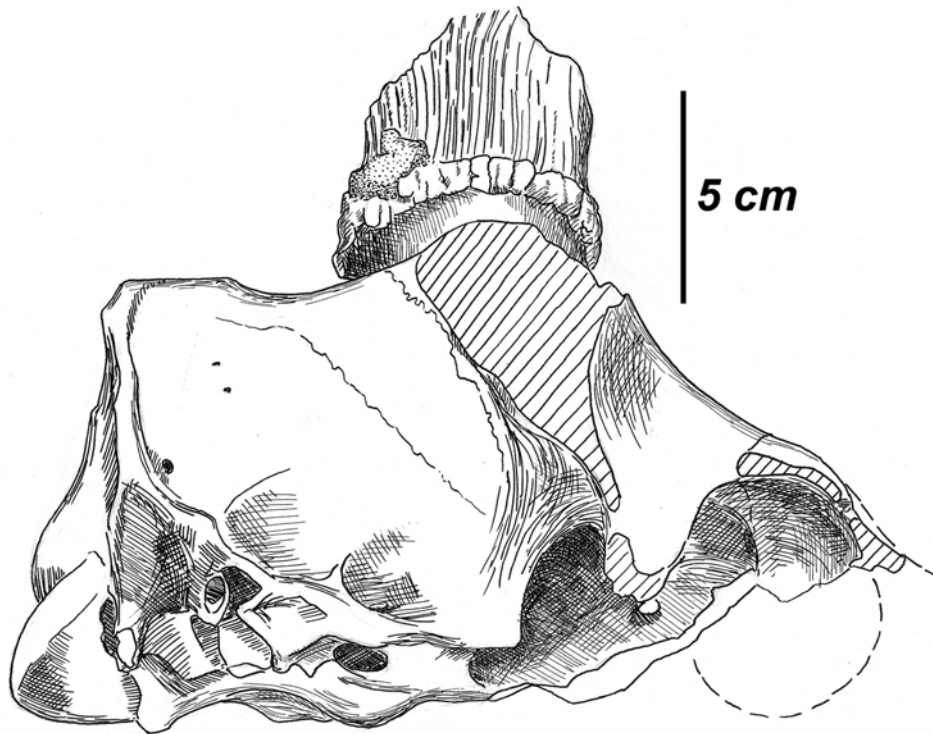


Fig. 2 - *Praemegaceros (Orthogonoceros) pliotarandoides*: side view of skull KM388.

DISCUSSION

Paleobiology. Large-sized deer represent a special ecotype of the family Cervidae that became important in Eurasian mammal assemblages from the Late Pliocene. Large body size and opportunistic feeding behaviour, with tolerance to high content of cellulose fiber in the forage, characterized this new ecological type of cervids. They represented an important evolutionary novelty allowing deer to occupy new ecological niches in open dry environments (Geist, 1998; Brugal & Croitor, 2007). Besides the large body size (*Praemegaceros* weighed about 400-500 kg, almost twice the body mass reached by *Eucladoceros*), among the evolutionary acquisitions of *Praemegaceros* should be mentioned the advanced

dentition with molarized P₄, the large complicated antlers that lost the archaic metameric pattern seen in the primitive closely related *Eucladoceros*, and the large palmations in the distal part of antler that evolved in the most advanced species of the genus. The giant deer ecotype is better adapted to low-quality fibrous forage due to the advanced morphology of the dentition and to the larger body size associated with lower rate of metabolism that allowed sustaining on forage of comparatively lower quality (Croitor & Brugal, 2007). The antler morphology may suggest some details of deer biology and ecology. *Praemegaceros pliotarandoides* is one of the primitive representatives of the genus that is characterized by advanced molarization of P₄ and antlers

Measurements (mm)	KM388 (sin)	KM388 (dx)
Postero-medial height of pedicle	39.2	
Antero-posterior diameter of pedicle	54.5	
Latero-medial diameter of pedicle	66.8	
Antero-posterior diameter of antler base	66.2	
Latero-medial diameter of antler base	73.2	
Antero-posterior diameter of burr	85.4	81.5
Latero-medial diameter of burr	89.2	87.7
Circumference of pedicle	195.0	
Circumference of antler base above pedicle	210.0	
Lateral height of the first ramification		102.0
Maximal diameter of the first tine base		51.0
Minimal diameter of the first tine base		48.0
Length of the IVth antler segment		200.0
Antero-posterior diameter of the antler segment IV		63.0
Latero-medial diameter of the antler segment IV		45.0

Table 2 - Measurements of antlers of *Praemegaceros pliotarandoides* specimen KM388 stored in the Regional Museum of Krasnodar (Russia).

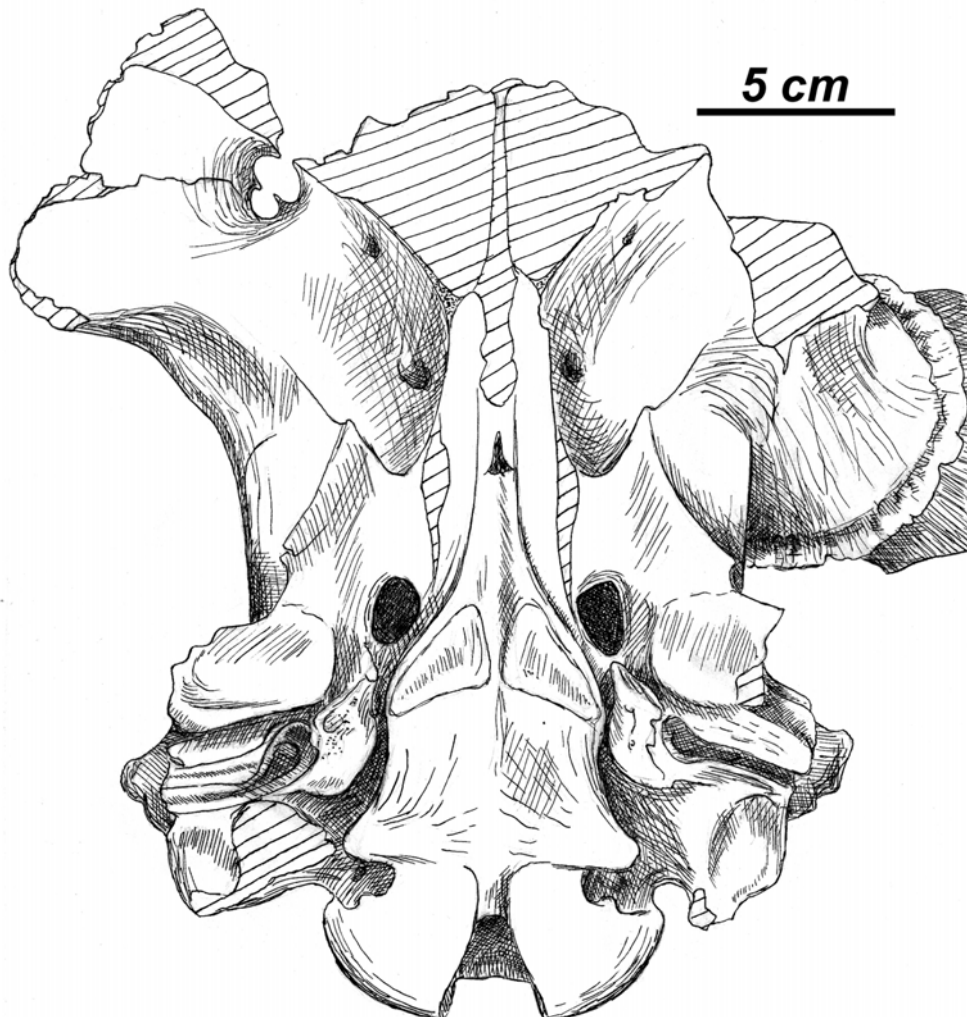


Fig. 3 - *Praemegaceros (Orthogonoceros) pliotarandoides*: dorsal view of skull KM388.

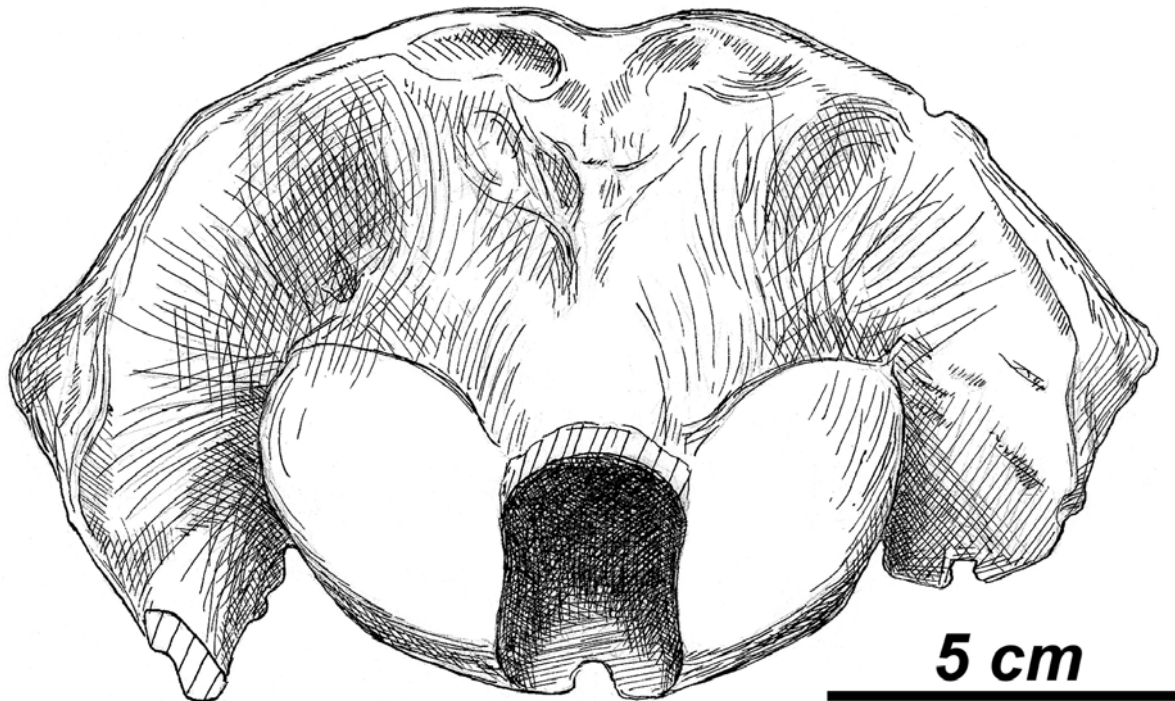


Fig. 4. *Praemegaceros (Orthogonoceros) pliotarandoides*: occipital view of skull KM388.

with simple dichotomous branching of crown tines (Radulesco & Samson, 1967; Croitor & Kostopoulos, 2004). The antler beam is directed backward and sideward as shown on the reconstruction (Fig. 6). The distal portion of the antler above the posterior tine is set upright on the antlered skull. The large size and wide lateral span of antlers suggests that the deer could not live in dense forests. The so called “outer” tine is directed toward the anterior on the antlered head of the deer. If compared to other species of the genus *Praemegaceros*, antlers of *P. pliotarandoides* tend to have reduced proximal tines (with subbasal tine almost disappeared) and missing middle tine. They apparently represent rather ritualized type of weapon, lacking well-developed proximal tines - a protection of the head against wounding inflicted by rival's antlers - as well as middle tine that fix the rival's antlers at a safe distance from the head (Lister, 1994; Geist, 1998). Antlers of *P. obscurus* differ in large, even hypermorphic proximal subbasal and dorsal tines and well-developed middle tine (Abbazzi, 2004; Croitor, 2006a) are present. The antlers of *P. obscurus* represent a sort of weapon better adapted to ritualized combats with evolved maximal protection against accidental injury. *P. solilhacus* possessed the most specialized antlers with completely reduced protective proximal tines and the broad distal palmation evolved (Azzaroli & Mazza, 1992a; Abbazzi, 2004; Croitor, 2006a). The antlers of *P. solilhacus* represent a good example of social specialization display that implies the ritualized social behaviour excluding violent combats between males (Geist, 1998).

The large posterior tine seen in *P. pliotarandoides* may be also indicative of open landscape adaptation. The posterior tine is found in modern open-landscape species *Rangifer tarandus* and in fossil giant forms *Sinomegaceros yabei* and *Megaloceros giganteus* assumed to be

specialized open-landscape forms (Geist, 1998). Obviously, the posterior tine evolved independently in each of the mentioned species. Possibly, the posterior tine situated at the sharp upright curving of the antler beam was used by the animal for back scratching to get rid of blood-sucking parasites. The specific adaptations against flying ectoparasites are found in large-sized open landscape herbivores like, for instance, the long hair tail in horses and large bovinds.

Based on the available fossil material (Croitor, 2006a), it can be stated that all mainland deer of the genus *Praemegaceros* are characterized by similar postcranial morphology and proportions as morphological traits related to the large body size, suggesting similar ecology. Among specific size-related features (see discussion in Gambarian, 1972) in giant cervids, one should mention the relatively short metapodials, the relatively long proximal limb bones, and the increased surface area of supporting joints (elbow joint, carpo-metacarpal joint).

Model of evolution. Three species of *Praemegaceros* found together in the Tamaian fauna represents a special phenomenon that needs an explanation. Perhaps, the most reliable explanation should be sought in the speciation pattern of *Praemegaceros*.

According to Azzaroli & Mazza (1992a, 1993) the general analogy of antler construction in *Eucladoceros boulei* from China and primitive European species of the genus *Praemegaceros* is obvious. It is reasonable to assume that *Praemegaceros* derived from a primitive *Eucladoceros* form similar to *E. boulei*. Surprisingly, remains of a deer similar to *Eucladoceros* from China were reported from the opposite part of the Eurasian mainland.

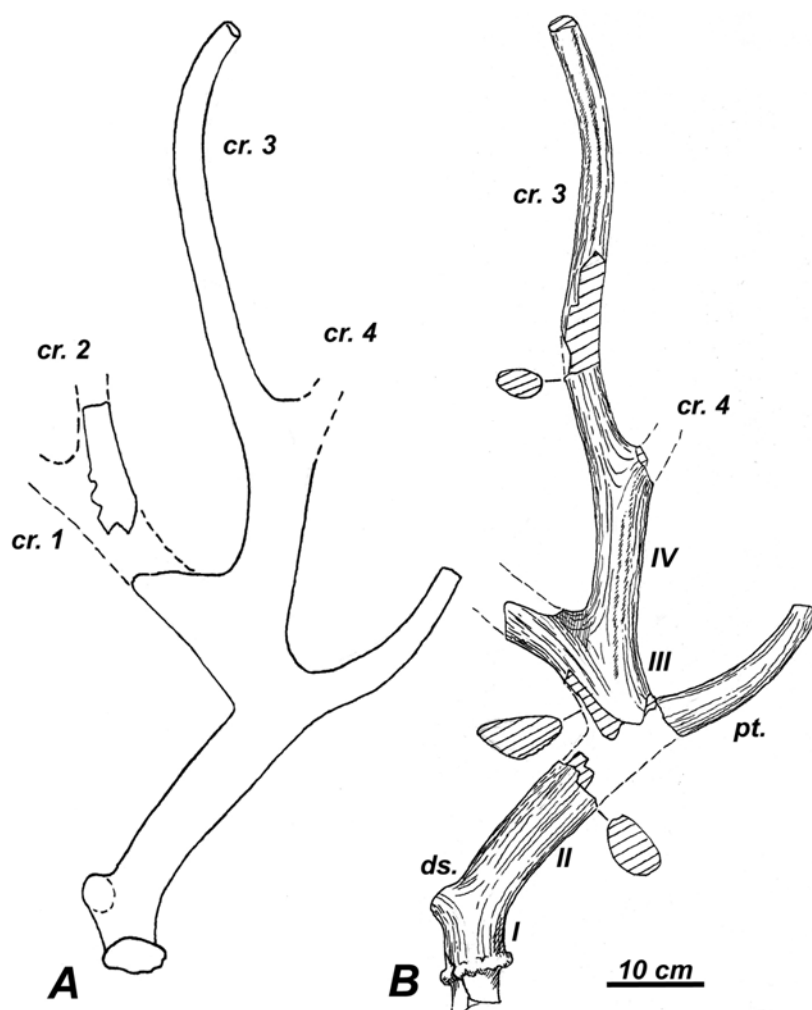


Fig. 5 - Right antler of specimen KM388: A, outline drawing of the antler made by Burchak-Abramovich (unpublished); B, antler reconstruction proposed in this study; *ds.*, dorsal tine; *cr. 1*, first crown tine; *cr. 2*, second crown tine; *cr. 3*, third crown tine; *cr. 4*, fourth crown tine; *pt.*, posterior tine; *I*, first segment of the antler beam (between burr and dorsal tine); *II*, second segment of the antler beam (between dorsal tine and posterior tine); *III*, third segment of the antler beam (between posterior tine and first crown bifurcation); *IV*, fourth segment of the antler beam (between first and second consecutive crown bifurcations).

Steensma (1988) described an almost complete antler of *Eucladoceros* aff. *boulei* from Kapetanios (Greece). The antler from Kapetanios has the typical *Eucladoceros* comb-like structure, but it is clearly different from that of the European species *E. ctenoides* and *E. dicranios*. It is much more robust and flattened with rather short and straight crown tines, and the crown tine metamery, unlike in the European species, is not regular. Perhaps, *Eucladoceros* from Kapetanios represents the episode of initial arrival of the genus in Europe from Asia. The arrival of *Eucladoceros* in Europe occurred before 2.5 Ma, while by this time well-evolved *E. ctenoides* in Western Europe (Saint-Vallier, Cornillet) (Heintz, 1970; Heintz & Dubar, 1981) and *E. dicranios* in Eastern Europe (Liventzovka) (Baigusheva & Titov, 2004) are already known. *P. pliotarandoides* from Psecupsian fauna dated back to ca. 2.2 Ma (Tesakov, 1995) is the earliest *Praemegaceros* recorded in Europe. Remains of *Eucladoceros* sp. and *Praemegaceros* sp. are reported also from Late Pliocene and Early Pleistocene of Tadjikistan respectively (Vislobokova, 1988).

The area of distribution of the genus *Eucladoceros* in the Late Pliocene seems to be continuous from Western

Europe to Eastern China (Fig. 7A) (Vislobokova, 1990). Apparently, various local populations of *Eucladoceros* were exposed to different selection pressures, which became more contrasting with gradual climate deterioration during Late Pliocene and Early Pleistocene. Obviously, natural zoogeographic barriers significantly influenced the differentiation of species. Among the important paleozoogeographic barriers, are the Alpine Mountain Chain that limited the distribution of cervids southward (Heintz et al., 1990) and participated in the fragmentation of their area of distribution, as well as the Parathetys Basin, which divided the initial area of distribution of *Eucladoceros* into the European and the Asian parts (Fig. 7A, B).

By the beginning of the Pleistocene, the distribution of genus *Eucladoceros* becomes broken: the distribution of *Eucladoceros* is confined to Western Europe and the eastern part of China. One can assume that progressive Late Pliocene climate aridization and cooling had a stronger impact in the Eurasian heartland that caused a deeper effect on cervid evolution. Archaic *Eucladoceros* with comparatively simple antlers and primitive dentition survived longer in those parts of Eurasia (like Western

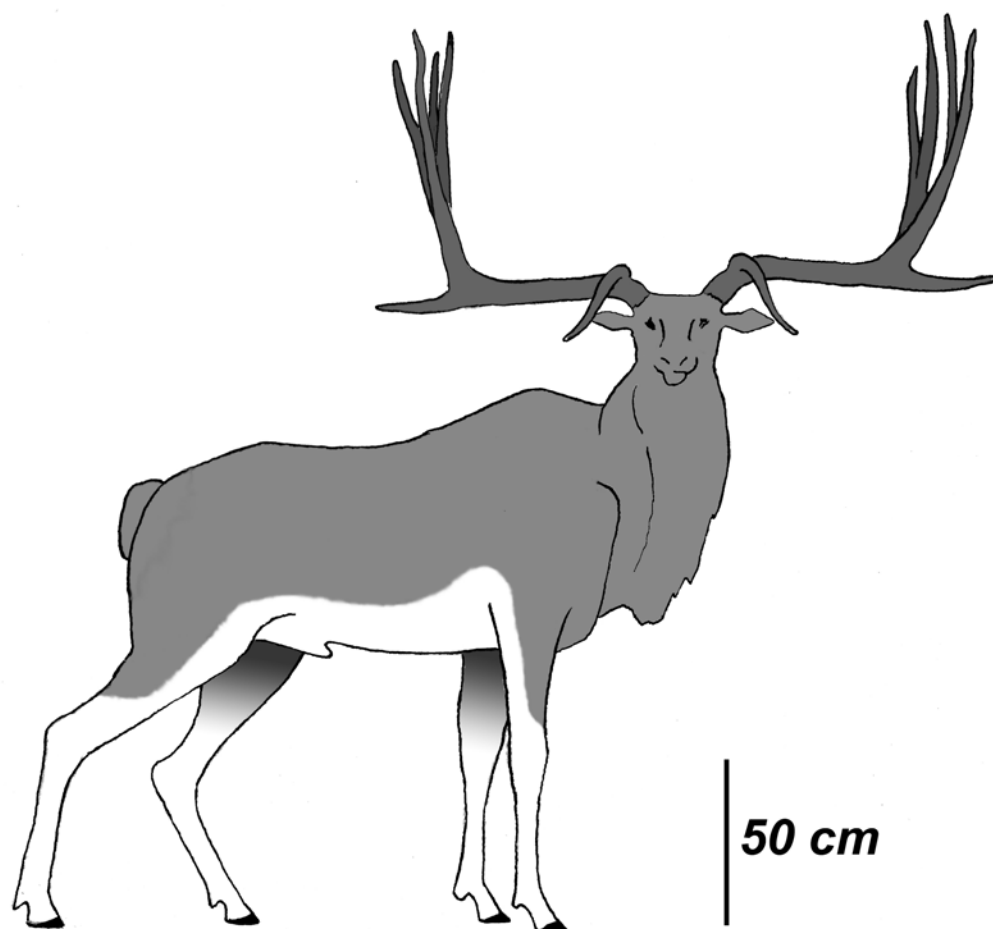


Fig. 6. Reconstruction of an antlered male of *Praemegaceros* (*Orthogonoceros*) *pliotarandoides*. The reconstruction of antlers is based on the specimen from Aliakmon (Greece) published and figured by Melentis (1967).

Europe and Eastern China) characterized by a comparatively milder climate mitigated by the ocean influence. Two sister species of *Eucladoceros* evolved in Europe: *E. ctenoides* with simple comb-like antlers in Western Europe (it is unknown from Eastern Europe and Asia), and *E. dicranios* with large, richly-branched antlers. Its antlers maintain taxonomically meaningful comb-like construction pattern, but each antler tine is bifurcated. The earliest remains of *E. dicranios* are known from Eastern Europe, however this species spread into Western Europe by the Early Pleistocene (Azzaroli & Mazza, 1992b; Vos et al., 1995; Croitor & Bonifay, 2001).

Most probably, *Praemegaceros* evolved in the dry continental climate conditions of Central areas of Asia. Perhaps, the Akchagilian Basin was the main geographical barrier that separated *Eucladoceros* from Europe and early *Praemegaceros* from Central Asia (Fig. 7B). The mosaic combination of morphological characters of the antlers suggests that *Praemegaceros* is a paraphyletic genus and consists of three closely related sister lineages that - in our opinion - may be regarded as subgenera: *P.* (*Praemegaceros*) with *P. obscurus* and *P. dawkinsi*; *P.* (*Orthogonoceros*) with *P. pliotarandoides* and *P. verticornis*; and *P.* (*Nesoleipoceros*) with *P. solilhacus* and *P. cazioti* (Croitor, 2006a).

Therefore, the Late Villafranchian *Eucladoceros* species and the subgenera of *Praemegaceros* are sister lineages that evolved from a primitive *Eucladoceros* form with a vast Eurasian distribution. The difference between Early Pleistocene *Praemegaceros* and *Eucladoceros* resulted from the high evolutionary rates and specific natural selection in *Praemegaceros* lineages in the less favorable conditions of climate continentality, open landscape and dry seasonal environment. *Eucladoceros* survived in regions with mild climate maintaining conservative primitive morphology and biology. By the beginning of the Pleistocene, the climate deterioration and the disappearance of the Akchagilian geographical barrier were followed by the expansion of Asian ruminant species into the Western regions of Eurasia with comparatively milder climate (Croitor & Brugal, 2007). The climate-driven migrations from East to West caused the overlapping of the area of distribution of *P. pliotarandoides*, *P. solilhacus*, and *P. obscurus*, and may explain their simultaneous presence in the same fauna. The presence of three *Praemegaceros* species representing the same ecotype in the composition of the Tamanian fauna is a peculiar phenomenon that needs discussion.

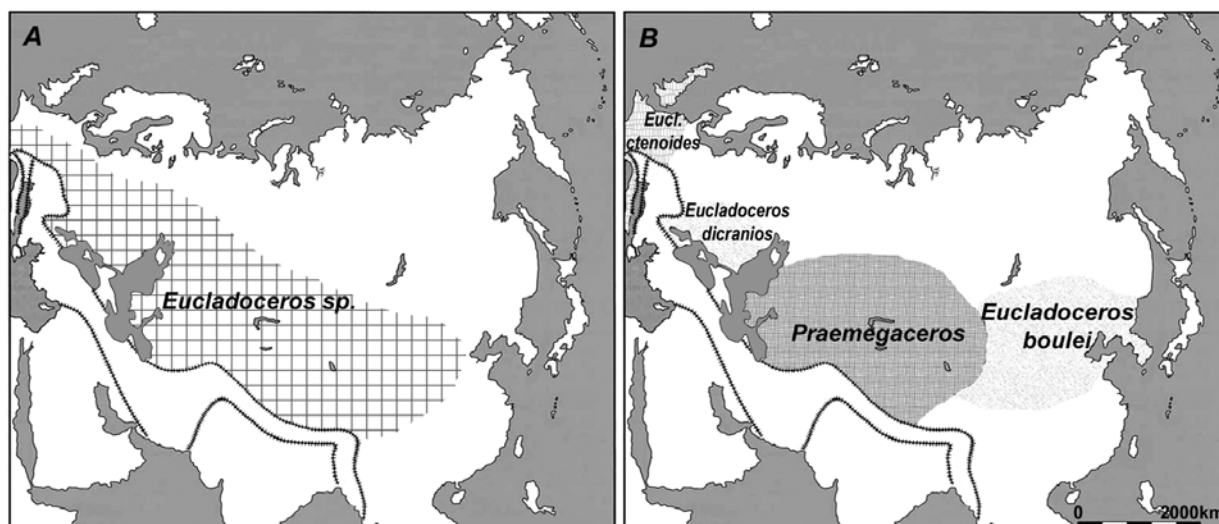


Fig. 7. Map showing the most important biogeographic obstacles (Euro-Asiatic Alpine Mountain Belt and Parathetys Basin) to the hypothesized distribution of *Eucladoceros* and *Praemegaceros* during the Late Pliocene: A, vast Euro-Asiatic distribution of a primitive eucladocerine form during the early Late Pliocene; B, fragmentation of the initial area of distribution of the eucladocerine forerunner form and emergence of descent sister species of *Eucladoceros* and *Praemegaceros* separated by the Akchagilian Basin.

Although the fragmentary character of the fossils does not permit complete and detailed ecological characteristics of *Praemegaceros* species from Tamanian fauna to be defined, the antler morphology and area of distribution of each species suggest quite different ecological needs. Antlers have an important social and behavioural function and represent the cervid body part that is best documented in the paleontological record. *P. pliotarandoides*, *P. solilhacus*, and *P. obscurus* are characterized by different type of antler morphology, suggesting different social and reproduction behaviour. Therefore, different shape and function ensured the reproductive isolation among the species and permitted their simultaneous presence in the same fauna. Possibly, *P. obscurus* was the most ecologically flexible species, since its vast area of distribution ranged from Near East to England (except for the Iberian Peninsula) (Croitor, 2006a). Its antlers represented an effective weapon for ritualized combats between males, with well-evolved adaptations against accidental wounding. Perhaps, this species was the most territorial among *Praemegaceros* and stronger tied to wooded biotopes. *P. pliotarandoides* seems to have been adapted to more open and dry countries. Its antlers are more specialized for display function and do not protect enough during intraspecific combats. This is the only *Praemegaceros* species that colonized the droughty Iberian Peninsula (Martínez-Navarro et al., 2003). *P. solilhacus* possessed the most specialized palmed antlers with pronounced function of visual display. This was an open landscape form with the most restricted area of distribution among the compared species that includes France, Italy, Moldova, and Tamanian Peninsula (Croitor, 2006a). Therefore, *P. pliotarandoides*, *P. obscurus* and *P. solilhacus* could coexist in the Tamanian fauna due to the reproductive isolation and the ecological partition among them.

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