Quaternary International 284 (2013) 110–122

Contents lists available at SciVerse ScienceDirect

Quaternary International

journal homepage: www.elsevier.com/locate/quaint

Large deer from the Villafranchian of Eastern Europe (Sea of Azov Region): Evolution and paleoecology

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ARTICLE INFO

Article history:
Available online 9 April 2012

ABSTRACT

The most numerous forms of large deer *Eucladoceros* and *Arvernoceros* from Villafranchian localities of Sea of Azov Region and adjacent territories are described. Their characteristics of evolutionary changes in a structure of their antlers are marked. The partial revision of late representatives of genus *Eucladoceros* with allocation of some subspecies was carried out.

1. Introduction

Deer are one of the index fossils in addition to other herbivorous mammals in continental beds of Eastern Europe, including areas of the Sea of Azov Region. The taxonomy of fossil deer is based mainly on features of their antlers. Taphonomical peculiarities result in antlers of adult animals being more often preserved in fossil condition. Deer are interesting for paleontology and paleoecology because they react to landscape changes more precisely than do elephants and horses. They are attached to a narrower ecological niche, as they are mainly browsing animals. The considerable variability of antler characteristics does not reduce their significance for biostratigraphy. In the Villafranchian in southeastern Europe, finds of remains of large deer of two lineages, *Eucladoceros* and *Arvernoceros*, are usual. They are known from the Khapry (Middle Villafranchian), Psekups (Middle-Late Villafranchian) and Taman (Late Villafranchian-early Galerian) Faunistic complexes.

The Khapry Faunistic complex is characterized by the presence of *Pliocrocuta perrieri*, *Homotherium crenatidens*, early meridionaloid elephants *Archidiskodon meridionalis gromovi*, late *Anancus arvernensis alexeevae*, the abundance of large and slender *Equus* (*Allohippus*) *livenzovensis*, *Elasmotherium chaprovicum*, and small *Paracamelus alutensis* (Gromov, 1948; Baygusheva, 1971; Titov, 2008). Most bones occur in the bottom of alluvial cross sections of the Khapry and Liventsovka sand pits. Remains of small mammals from these layers allow dating the Khapry Faunistic complex as Late Villanyian, zone MN 17 (Tesakov, 2004). There are rather numerous remains of *Eucladoceros dicranios tanaitensis* subsp. nov. and *Arvernoceros* cf. *verestchagini*, beside the small deer *Cervus* (*Rusa*) *philisi*. The analysis of the association indicates the presence of a warm and relatively dry climate with hot summers and slightly snowy winters with weak cold weather, warmer and drier, than the modern ones. The absence of forms adapted to drought habitats, and the abundance of species typical for open and semi-open landscapes, indicates the nearest (not full) analogue of this fauna is from the modern African savanna.

For the Psekups (Odessa) Faunistic Complex, which can be considered as a later stage development of the Khapry, the presence of *Archidiskodon meridionalis meridionalis*, *Stephanorhinus* cf. *etruscus*, and *Equus* (*Allohippus*) cf. *major* were typical. During this period *Anancus* and *P. alutensis* continue to exist, but become less numerous. For the first time, *Bison* appeared. Among deer, *Eucladoceros orientalis orientalis* subsp. nov. and *Pseudodama nestii* are characteristic. During this period *Anancus* and *P. alutensis* continued to exist, but become less numerous. For the first time, *Bison* appeared. The most representative fauna of this type occurs from Ciscaucasus (sites Saratovskaya and Bakinskaya) from the bases of the Psekups riverbank sections. Deposits with Psekups fauna belong to an early part of the Matuyama epoch, and small mammal fauna indicate the end of Villanyian, and early Upper Villafranchian, to the end of zone MN 17 (Tesakov, 2004). Probably, an intensification of aridization and widening of steppe-like areas occurred. However, there were no radical reorganizations in the structure of large mammal association in comparison with the previous stage. From this time, “savanna-type” Eurasian landscapes began to be transformed to the present steppe and forest-steppe.

The Late Villafranchian-early Galerian Taman Faunistic Complex was characterized by *Canis tamanensis*, *Canis* (*Xenocyon*) *lycaonoides*, *Ursus* sp. *Lutra simplicidens tamanensis*, *Pachycrocuta*

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doi:10.1016/j.quaint.2012.04.001

brevirostris, *Panthera* sp., *Homotherium latidens*, *advanced southern elephants Archidiskodon meridionalis tamanensis*, *Stephanorhinus* cf. *etruscus*, *Elasmotherium caucasicum*, *Equus* (*Allohippus*) *major*, *Sus* cf. *strozzii*, *Bison tamanensis*, *Pontoceros ambiguus*, *Tragelaphus* sp., and *Gazella* sp. (Vereshchagin, 1957; Baygusheva, 2000; Sotnikova and Titov, 2009). Among large deer, the most usual is *E. orientalis pliotarandoides* subsp. nov. Microtheriofauna from these sites is early Galerian and Early Biharian (Tesakov, 2004). Most Epivillafranchian sites with large mammals include alluvial, deltoid and lagoon deposits of the Taman Peninsula and northern Sea of Azov Region, indicating significant water-dominated territories. They represent the first half of this period, which was characterized by a warmer climate interpreted as rather damp, close to subtropical. Such a spectrum of animals specifies a variety of biotopes, ascribed to steppe and forest-steppe landscapes, and the absence of psychrophilic elements. The dominating forms of large mammals in taphocoenoses of the Taman Faunistic Complex were inhabitants of semi-open and open habitats: elephants, deer, horses, and bison.

There is no uniform established system of proximal tine designation for antlers of bush-antlered deer. Azzaroli (1953) designated the first tine, which branches off above the antler's burr in *Eucladoceros* (*Euctenoceros*), as "the brow" tine. Abbazzi (2004) use the definitions 'first' and 'second basal tine'. The same system was followed by Radulesco and Samson (1967), as tine 1 and tine 2. Heinz (1970) numbered tines in order from proximal to distal ones. Kahlke (1956) named these tine A and tine E, respectively. Several researchers (Azzaroli and Mazza, 1992, 1993; de Vos et al., 1995) call the first tine, situated above the burr and some laterally, as "outer tine". The second tine which deviates from the beam somewhat higher than the first and medially was designated as the "inner tine". A serious attempt to unify the titles of these processes was made by Croitor (2006). However, he caused significant confusion with the name of the proximal processes. Trying to separate characteristics of *Eucladoceros* and *Praemegaceros*, he singled out the notions of basal/subbasal tines and dorsal tine. Croitor did not consider the "medially situated basal tine" in *Praemegaceros* as the homologue of the outer tine in *Eucladoceros*.

However, taking into consideration the extremely low position of the first lateral tine in adult individual *Eucladoceros* antlers from Liventsovka, it is quite difficult to distinguish subbasal and basal tines using the system of Croitor (2006). This approach is inconvenient for describing fragmental and undetermined material. Given the evidence of age variation on the antlers of *Eucladoceros* from Liventsovka sand pit, the following system was used for the two lower tines' names. The first tine, situated above the burr on the front side of the beam or laterally, is a basal tine. In some forms, it can be reduced to a state of button-like vestige. The upper tine, located on the front (dorsal) side and somewhat displaced medially, is the dorsal tine. In some forms it can be greatly reduced, whereas in other deer, it can be represented by a lesser single or double tine. Distal tines which are located on the bar are crown tines. In *Praemegaceros* a medial tine is usually present (Croitor, 2006). The system of antler measurements was taken from Heintz (1970): for *Eucladoceros* according to Heintz's fig. 202, 208, and for *Arvernoceros*, Heintz's fig. 304, 305.

2. Systematic paleontology

Family Cervidae Goldfuss, 1820
Subfamily Cervinae Goldfuss, 1820
Tribe Cervini Goldfuss, 1820
Genus *Eucladoceros* Falconer, 1868
Eucladoceros dicranios (Nesti, 1841)
Eucladoceros dicranios tanaitensis Baygusheva and Titov ssp. nov.
1948 *Cervus* ex gr. *polycladus*; Gromov, 45
1971 *Eucladoceros dicranios*; Baygusheva, 23; pl. 6(4, 5)
1984 *E. dicranios*; Baygusheva, 168
1990 *Eucladoceros dicranios*; Vislobokova, 186
1994 *Eucladoceros* cf. *dicranios*: Baygusheva, 237; fig. 1–4
2008 *Eucladoceros* sp.; Titov, 123–132; pl. 9(1–3)

Holotype: incomplete right antler, Rostov-on-Don Local Museum (ROMK), L-531.

Type locality: Liventsovka, Rostov Region, Russia, Khapry alluvial layers.

Age of the type locality: Lower Pleistocene, Middle Villafranchian, Khapry Faunal Complex.

Material: skull fragments with antlers (8 specimens), 27 fragmentary antlers, 4 lower jaws, 22 limb bones; collections of AMZ, ROMK, PIN, GGM.

Etymology: in reference to the Tanais, the ancient name of the Don and Seversky Donets rivers.

Differential diagnosis: antlers differ from the same of nominative subspecies by the absence of a significant curving of upper antler's branches backwards and by more flattening tines. The index of beam flattening in adult individuals (the ratio of width of the section to its anterior-posterior diameter) is 0.73–0.92 (on the average 0.84), and for crown tines (at its base) – 0.57–0.68 (on the average 0.61).

Description: Characteristic features of the skulls are as follows: frontal surface is weakly concave behind the eye sockets; interfrontal sagittal suture is flat, in young individuals - more convex; cerebral post pedicle part of the skull is wide and short; mastoid bone is sub-rectangular, rather narrow, oval foramen is small, occiput rather high (Table 1, Fig. 1d–f); supraoccipitale trapezoid, convex, occipital crest short; fossa nuchalis distinct.

Pedicles are massive, rounded in section. In older individuals, they are shorter and more massive (Tables 2, 3). The angle of pedicles divergences in young animals makes 70°, and in adults reaches 85°. The distance between the bases of pedicles is equal or less than the pedicle's width (0.73–0.8). Axes of a pedicles' divergence are directed latero-caudally.

Antlers are large (Fig. 2). Burr is massive and rounded. The bases of antlers are from oval to subtriangular in cross section. On the anterior side of the beam is the first basal tine (according Croitor, 2006; outer tine according to Azzaroli and Mazza, 1992) situated somewhat laterally. In adult animals with large antlers, the basal tine is implanted low, almost near the burr. In young animals, this tine is usually located on some distance from the burr, and it is rather long, rounded in cross section. Usually it is not ramified, a little bit declined laterally, and turned up. In old individuals the basal tine is flat, in cross section from oval to subtriangular. Probably, in adult animals the palmation was formed on the end of this tine. On the antlers of mature forms, there is an unbranched round in cross section of the dorsal tine (according to Croitor, 2006; inner tine according to Azzaroli and Mazza, 1992). On the specimen ROMK L-247, there are two. In young forms this basal tine is expressed by a knob. Above the dorsal tine the beam deviates back and sideways under an angle of 83–135°. All crown tines are implanted to the anterior surface of the beam and dichotomy bifurcated. The cross section of the burr varies from rounded to subtriangular, and it flattens distally. The antler's surface is rough-striated.

Upper teeth are subhypsodont, narrowed from the basis to a chewing surface. The ventral margin of the mandible is relatively straightforward. The lower teeth have a structure typical for Cervidae. The lower premolars are weakly molarized. Teeth p2 have the first stage of molarization, and p3 – the second (Heintz, 1970). Metaconids are connected with protoconids. Teeth p4 are of the third stage of molarization. Metaconid is extended in an anteroposterior direction. Entoconid and entostylid are oblique

Table 1
Skull measurements of some representatives of *Eucladoceros* from the Sea of Azov Region.

Measurements, mm	*Eucladoceros dicranios tanaitensis*		*Eucladoceros orientalis orientalis*	*Eucladoceros orientalis pliotarandoides*		
	Liventsovka		Bakinskaya	Taman peninsula	Semibalki	Tsimbal
	ROMK L-379	ROMK L-1600	PIN 4378/1, destroyed	KKM 388	AMZ OP-818	ZIN 26001
Mastoid width	130.0	–	170.0	160.0	142.0	143.4
Interorbital width	131.0	148.0	170.0	172.0	171.0	161.2
Braincase length behind pedicles	(85)	–	–	79.2	80.8	81.6
Braincase width behind pedicles	110.4	127.0	–	127.4	123.4	117.8
Distance between upper lateral part of pedicles	(176)	195.0	–	195.0	183.0	183.8
Distance between bases of pedicles	37.8	43.2	–	44.0	40.0	38.0
Width of occipital condyles	76.0	–	–	93.0	96.0	94.2
Width of occipital restriction in front of the occipital ridges	44.4	–	–	53.6	53.4	(58.8)
Width of ventral notch of occipital condyles	5.0	–	–	9.0	8.0	7.0
Occipital height	88.0	–	73.0	105.0	97.2	99.0
Lacrimal bone length	–	–	75.0	–	–	–
Lacrimal bone width	–	–	44.0	–	–	–
Nasal length	–	–	143.0	–	–	–
Nasal width	–	–	57.0	–	–	–
Hyatus nasolacrymale length	–	–	57.0	–	–	–
Hyatus nasolacrymale width	–	–	34.0	–	–	–
Angle of pedicles' divergence, °	80	83	(80)	85	90	80

posteriorly. Entostylid is relatively large. Paraconid is usually well expressed. On some teeth, paraconid and an anterior part of metaconid are pulled strongly together. On the lower molars the protostylids are well developed. Additional columns (ectosylids) are well advanced, mainly on m1.

Comparison. The obviously expressed dichotomy bifurcation of antlers relate *Eucladoceros* from Khapry layers to *E. dicranios* Nesti from Upper Valdarno, *E. sedgwickii* Falconer from Norfolk (Great Britain), *Eucladoceros orientalis* (Radulesco et Samson) from Psekups (st. Bakinskaya), and *Eucladoceros pliotarandoides* from the Sea of Azov Region (Ukraine), Italy, and Greece. The presence of dichotomy ramification of crown tines is observed in some *E. boulei* Teilhard et Piveteau (Heintz, 1970). By this property, *Eucladoceros* from Liventsovka differs from *E. tetraceros* Dawkins and *E. ctenoides* Nesti, including from *E. "senezensis"* Deperet (= *E. ctenoides*), and *E. "teguliensis"* (Dubois) (= *E. ctenoides*; de Vos et al., 1995).

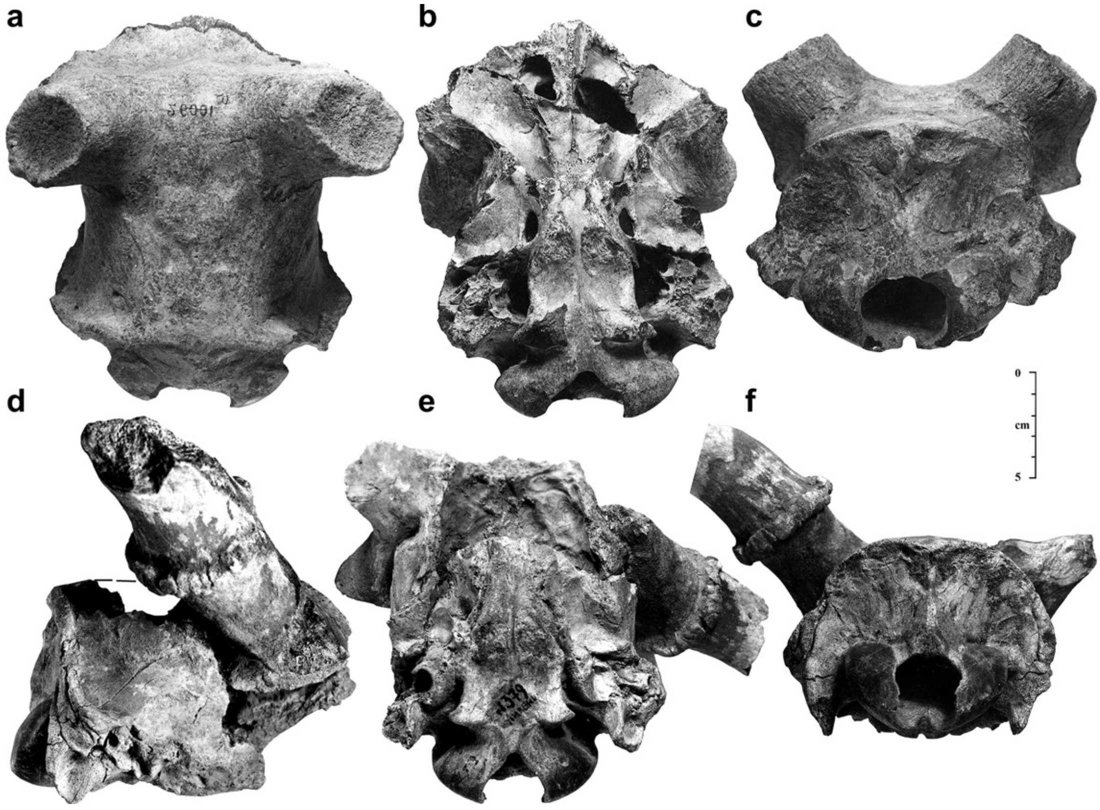

Fig. 1. *Eucladoceros orientalis pliotarandoides* from Tsimbal sand pit (Taman peninsula, Sea of Azov Region; late Early Pleistocene, Late Villafranchian), braincase (ZIN 26001): (a) dorsal view; (b) ventral view; (c) posterior view; *Eucladoceros dicranios tanaitensis* from Liventsovka sand pit (North-Eastern Sea of Azov Region; early Early Pleistocene, Middle Villafranchian), braincase (ROMK L-379): (d) lateral view; (e) ventral view; (f) posterior view.

Table 2

Antlers' parameters of *Eucladoceros* from the Sea of Azov Region. MAD – mean absolute deviation, – standard deviation. Data in parenthesis are approximate.

Measurements, mm	*Eucladoceros dicranios tanaitensis*								*Eucladoceros orientalis orientalis*	*Eucladoceros orientalis pliotarandoides*				
	ad, Liventsovka; coll. ROMK, AMZ			subad, Liventsovka; coll. ROMK, AMZ			Liventsovka, all		Psekups	Taman peninsula	Semibalki	Mariupol		Tsimbal
	n	min–max	M	*n*	min–max	M	MAD	*δ*	PIN 4378/1	KKM 388	AMZ OP-840	MKM-I-864	MKM-I-435	ZIN, No. 26001
Burr diameter latero-medial (1)	6	60.5–70.0	64.6	9	40.2–72.6	57.9	5.80	7.86	60.0	89.2	70.6	(64)	–	–
Burr diameter anterio-posterior (2)	6	65.6–80.8	71.6	9	48.2–70.0	58.7	8.51	10.41	67.5	85.4	85.8	–	–	–
Pedicle height	3	28.0–42.8	34.3	4	24.4–39.4	30.9	3.73	4.51	–	–	–	–	–	–
Pedicle diameter latero-medial	3	50.4–55.5	54.1	7	39.2–47.0	43.7	3.90	5.61	(49)	66.8	–	–	–	43.0; 50.0
Pedicle diameter anterio-posterior	3	46.3–52.0	48.4	7	40.8–54.8	45.6	4.07	5.54	(55.5)	54.5	–	–	–	53.0; 59.5
Angle of first bifurcation, °	5	100–135	120	–	–	–	–	–	85	(100)	(90)	115	–	–
Length of first segment (length from the burr to distal end of dorsal tine base)	5	60.5–119.0	91.6	7	70.4–108.0	85.5	14.74	20.74	113.0	102.0	(107)	117.6	136.0	–
Length of second segment (length from dorsal tine to distal end of first crown tine base	1	201.0	–	–	–	–	–	–	(363)	(400)	–	410.0	–	–
Length of third segment		–	–	–	–	–	–	–	230.0	(198)	–	240.0	–	–
Antler's base diameter above the burr latero-medial (3)	6	52.3–60.8	57.15	9	39.8–56.2	47.8	6.22	7.50	47.2	63.0	56.0	–	–	–
Antler's base diameter above the burr anterio-posterior (4)	6	60.0–75.0	66.0	9	42.4–55.4	48.8	7.07	9.07	53.0	72.0	75.6	60.0	–	–
Basal tine's base diameter latero-medial	5	27.4–34.6	32.3	–	–	–	–	–	41.0	53.0	45.8	–	34.0	–
Basal tine's base diameter anterio-posterior	5	38.4–72.2	53.3	1	56.0	–	–	–	48.3	50.0	50.0	–	35.0	–
Length of basal tine		–			–	–	–	–	>164	–	–	(290)	–	–
Beam's diameter above the basal tine lateral-medial	5	39.5–47.0	44.1	4	25.6–56.2	40.6	–	–	52.0	54.0	–	–	48.0	–
Beam's diameter above the basal tine anterio-posterior	5	50.0–54.0	52.2	4	50.6–57.4	54.3	–	–	60.7	67.0	–	–	60.0	–
Index of flattering of the burr (1/2)	6	0.78–0.99	0.90	9	0.79–0.99	0.91	0.05	0.08	0.9	0.96	0.82	–	–	–
Index of flattering of the antler base (3/4)	6	0.7–0.99	0.87	9	0.79–0.95	0.88	0.07	0.09	0.9	0.88	0.74	–	–	–
Index of flattering of dorsal tine	5	0.5–0.72	0.63		–	–	–	–	0.8	0.94	0.92	–	0.97	–
Index of flattering of the beam	5	0.73–0.92	0.84	4	0.45–0.95	0.73	–	–	0.9	0.81	–	–	0.8	–

Table 3
Antlers' measurements of mature and young *Eucladoceros dicranios tanaitensis* from Khapry layers. Data in parenthesis are approximate.

Measurements, mm	L-531	Kh-400	L-247	L-575	L-1600	L-1218	L-882	L-2110	AMZ-1425	L-75	L-380	L-428	L-1559	L-1199	L-1510	L-1568	L-1661	L-1790
Burr diameter latero-medial	64.2	58.0	64.2	64.2	75.8	64.0	(52)	62.6	71.8	(40)	55.6	48.2	(40)	(50)	61.4	52.0	(52)	71.6
Burr diameter anterio-posterior	79.0	79.0	70.8	63.0	81.2	70.0	(53)	64.2	87.2	(42)	59.4	54.0	(51)	55.0	67.8	57.2	(52)	72.6
Pedicle height	–	26.8	33.0	27.2	34.6	27.2	30.2	34.0	31.0	–	30.8	24.4	–	36.4		39.4	36.8	27.0
Pedicle diameter latero-medial	–	50.4	50.4	54.0	54.0	47.2	48	45.0	51.8	32.2	47.0	40.8	–	45.0	46.8	45.0	48.0	54.8
Pedicle diameter anterio-posterior	–	49.8	46.0	54.0	56.0	49.0	44.2	45.0	54.0	33.4	46.6	41.4	–	44.0	50.0	45.6	42.6	45.8
Length of first segment (length from the burr to distal end of dorsal tine base)	62.2	60.6	93.6	130.0	85.4	78.4	128.4	93.0	90.8	55.0	84.0	74.8	82.3	67.0	95.0	84.6	70.4	–
Length of second segment (length from dorsal tine to distal end of first crown tine base)	201.0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Antler's base diameter above the burr latero-medial	59.6	(51)	56.8	53.2	58.2	45.4	44.2	48.0	50.8	36.0	52.2	41.8	39.8	44.6	43.8	48.2	45.8	53.2
Antler's base diameter above the burr anterio-posterior	63.0	74.8	63.2	60.4	72.2	54.4	43.4	53.0	63.0	46.0	45.8	49.0	49.6	48.8	55.4	52.0	48.0	56.2

de Vos et al. (1995) considered *E. sedgwickii* as a junior synonym of *E. dicranios*, based on the similarity of the structure of dichotomously branching antlers. However, there are a number of morphological differences in the structure of their antlers that give reason to consider them as separate subspecies of *E. dicranios*: *E. d. dicranios*, and *E. d. sedgwicki*. They are similar species, differing from other deer by the clear dichotomy of crown tines.

In the revision of the genus *Eucladoceros*, de Vos et al. (1995) made a number of assumptions that are disputable. For example, referring to the significant variation of the height of the "first tine" they asserted the unsuitability of this feature for specific diagnosis. However, they combine data from all *Eucladoceros* regardless of age variability. Observations which were made on the material from Liventsovka locality show a clear pattern of the first tine localization above the base of the antler, depending on the individual age. Variability with specimen age and individual characteristics of deer antlers is considerable. However, the holotypes of three *E. dicranios* subspecies are of similar age adult individuals, providing the possibility of full-fledged comparison.

The absence of published concrete measurements of antlers from Upper Valdarno and Norfolk makes it difficult to carry out direct comparison. However, according to Azzaroli (1953) who directly studied remains of both forms, deer antlers of *E. dicranios* (= *E. d. dicranios*) from the Late Villafranchian of Upper Valdarno differ from the same of Middle Villafranchian *E. sedgewicki* (= *E. d. sedgwicki*) from Great Britain by weak flattening of crown tines.

Antlers of Azov *E. d. tanaitensis* also differ from the same of the nominate subspecies by a greater flattening of crown tines. In addition, the better preserved antler in the Khapry fauna collection ROMK L-531 differs from that of typical *E. d. dicranios* by its lesser length. Moreover, on massive antlers from Liventsovka the first basal tine is situated near the burr, whereas on the specimen from Upper Valdarno it diverges higher on the beam. The angle of pedicle divergence is larger in the samples from the Khapry alluvium. The basioccipital is less massive and flattened. In general, the size of skulls from Liventsovka and Upper Valdarno is similar.

E. d. sedgewicki differs from *E. d. dicranios* and *E. d. tanaitensis* by the clearly highest location of the basal process. In addition, on the antlers of adult deer from Norfolk there is no obviously represented dorsal tine. As pointed out by Azzaroli (1953), the high position and the flattening of the first basal ("brow tine") tine are remarkably constant and well displayed in adult and in young specimens of *E. sedgewicki* (= *E. d. sedgwicki*).

From *E. boulei* from China, another deer with dichotomy bifurcation of crown tines, the deer from Sea of Azov Region are distinguished by the low position of the basal tine, more expressed dichotomy bifurcation, and smaller distance between basal and crown tines.

From *E. orientalis* (=*E. o. orientalis*) from Psekups, the form from Liventsovka differs by it bigger basal tine, lesser distance between proximal tines and crown ones, greater flatness of a beam, and smaller total antler length. The height of the first bifurcation of adult deer antlers from Liventsovka on the average is less, and the basis of an antler is more massive, than from Psekups. The angle between dorsal tine and beam prolongation is larger in *E. d. tanaitensis*. In *Eucladoceros* from Khapry layers, the height of the second ramification is less than at *E. pliotarandoides* (=*E. o. pliotarandoides*) from the Mariupol and Krasnodar museums.

Postorbital width of the skull, and the width of the occipital bone of Khapry specimens are less than that of *E. pliotarandoides* (=*E. o. pliotarandoides*) from Tsimbal (Taman Peninsula, Early Pleistocene). In the skulls from Liventsovka, the post pedicle part of the cranium is longer, with less pronounced facial fracture. The basioccipital bone of Liventsovka's deer is square, while at Tsimbal it is subtriangular. The divergence of pedicles is larger on average in the Khapry samples.

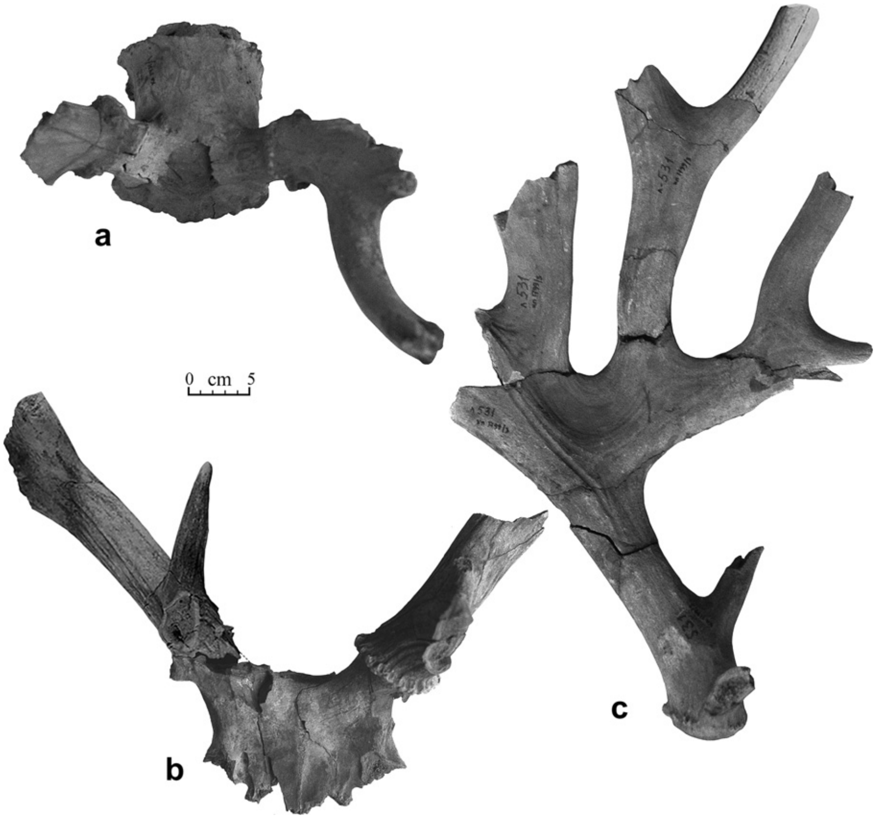

Fig. 2. *Eucladoceros dicranios tanaitensis* from Liventsovka sand pit (North-Eastern Sea of Azov Region; early Early Pleistocene, Middle Villafranchian): (a) braincase with fragments of antlers (ROMK L-1218): dorsal view; (b) the part of the skull with the fragment of left antler (ROMK L–1600), rostral view; (c), incomplete right antler (ROMK L-531): lateral view, holotype.

Eucladoceros orientalis (Radulesco, Samson, 1967)
Eucladoceros orientalis orientalis (Radulesco, Samson, 1967)

1948 *Cervus* cf. *pliotarandoides*; Gromov, 53
1959 *Eucladoceros pliotorandoides*; Verestchagin, 60–62; fig. 30
1962 *E. pliotarandoides*; Flerow, 373–374; fig. 492, 493
1967 *Psekupsoceros orientalis*; Radulesco and Samson, 332; fig. 5
1977 *Eucladoceros* sp.; Alexeeva, 127; fig. 24a
1990 *Eucladoceros orientalis*; Vislobokova, 158.
1992 *Megaceroides orientalis*; Azzaroli and Mazza, 27–28; fig. 3
1993 *M. orientalis*; Azzaroli and Mazza, 6–7; fig. 3
2004 *Praemegaceros pliotarandoides*; Croitor and Kostopoulos, 144, 154; fig. 14, 16a
2005 *Praemegaceros pliotarandoides*; Croitor, 90; fig. 4a
2006 *Praemegaceros (Orthogonoceros) pliotarandoides*; Croitor, 107; fig. 15
2009 *E. orientalis orientalis*; Baygusheva, 459–461; fig. 1

Holotype: incomplete right antler, Paleontological Institute RAS, PIN 4378/1.

Type locality: Bakinskaya, Krasnodar Region, Russia, blue clays of Psekups River.

Age of the type locality: late Lower Pleistocene, late Middle – early Late Villafranchian, late MN 17, Psekups Faunal Complex.

Material: a skull (nowadays destroyed) with an antler No. 4378/1, collection of PIN.

Description: The description of the skull PIN No. 4378/1 from Bakinskaya was made on the basis of K.K. Flerow's manuscript about the undestroyed skull. During the transportation from Leningrad to Moscow in the 1940s, the sample was destroyed and lost. Preorbital fossa is deep, well-defined, located at the greater part of the lacrimal bone (Table 1). Fossa lacrymale is of moderate depth. The nasal bones in comparison with *Cervus* are slightly shortened. Length of nasals is 85–90% of interorbital distance. Premaxilla with blade-like processes are in the anterior part of lateral edge. The divergence of pedicles is 80° (according to fig. 24a of Alexeeva, 1977, Fig. 3).

Antler is large with a massive burr. The total length of the antler PIN No. 4378/1 is about 1080.0 mm. At the base the cross section of the beam and tines are rounded, in distal parts they are slightly flattened (Table 2). The basal tine is reduced, shaped as a roughness (according to K.K. Flerow). The dorsal tine is implanted at some distance from the burr. This tine is straight at the base, diverges

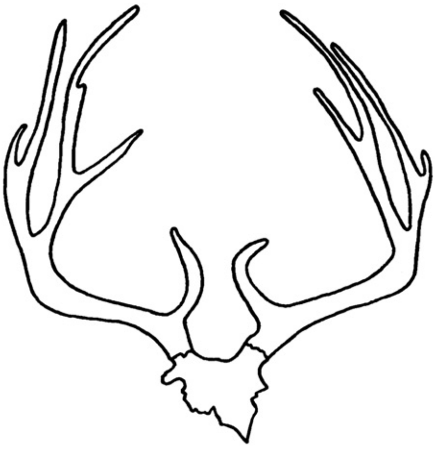

Fig. 3. The contours of deer antlers *E. orientalis orientalis* from the Bakinskaya locality (Psekups). A sketch was made from a photograph from the archive of V.I. Gromov (Alexeeva, 1977).

from the beam straight and slightly outward, and the end is turned slightly upward. A not quite correct picture of the antler and its incomplete description, which were given by Samson and Radulesco (1967), and reproduced in following publications (Azzaroli and Mazza, 1993; Croitor and Kostopoulos, 2004), brought a number of discords in the interpretation of the specimen. Because this species was described by the picture, a rather short pointed dorsal tine was depicted, although it was broken off, and really was longer. In addition, in the original antler a knob-like basal tine was noted, which was not rebuilt after the restoration. Crown tine at a considerable distance from the dorsal one are curved upwards and outwards, bifurcated into two branches, which bifurcated in their turn (Fig. 4a). The continuation of the beam after the crown tines is short, slightly curved upwards. Index of flattening of the beam is 0.9, and 0.68 of tines. The surface of the antler is covered with shallow longitudinal furrows.

The upper premolars have well developed metastylids. The upper teeth are narrowed from the basis to a chewing surface. There are additional columns, ectostylids. Maximal width of M2 at the base is 25.0 mm, and the chewing surface is 16.0 mm. The hypoconulid is well developed on the M3. The length of the M3 is 27.0 mm, width 25.0 mm. Length of tooth row P3-M3 at alveoli level is 125.0 mm.

Comparison. The presence of dichotomy bifurcation of antlers, and the different form of the dorsal tine of *Eucladoceros* from Psekups, well distinguishes this form from *E. tetraceros* and *E. ctenoides*. From *E. dicranios*, deer from Psekups differ by the unramified dorsal tine, large distance between basal and crown tines, less flattening of the beam, and less massiveness of the antler's base. *E. o. orientalis* differs from *E. boulei* by less flattening of the antler, larger angle of divergence of the dorsal tine and the beam, lower location of basal tine, and the weak development of the basal tine.

From the representatives of the tribe Megacerini, it differs by a rather large size of preorbital and nasolacrimal fossa, expressed ethmoidal fissures, and the absence of significant convexity of the mandible. From *Praemegaceros verticornis*, it differs by a structure of the supraorbital processes, the presence of a clear dichotomy of antlers, and other proportions of the skull.

Eucladoceros orientalis pliotarandoides (De Alessandri, 1903)

1903 *Cervus pliotarandoides*; De Alessandri, 11, fig. 4–5
1956 *Cervus* cf. *pliotarandoides*; Pidoplichko, pl. XXIV, fig. 3
1957 *Eucladoceros* sp.; Verestchagin, 51–53; pl. VII, 1–4, VIII, 1–3
1959 *Eucladoceros* sp.; Verestchagin, 63; fig. 34(9)
1965 *Eucladoceros pliotarandoides*; Gromova, 86–87
1967 *Orthogonoceros verticoruis*; Melentis, 79; fig. 2, pl. 1–2
1976 *Megaceros verticornis*; Azzaroli, 485; pl. 1–2
1977 *Eucladoceros* cf. *pliotarandoides*; Alexeeva, 127; fig. 24b
1993 *Megaceroides orientalis*; Azzaroli and Mazza, 6; fig. 3
2000 *Eucladoceros* aff. *orientalis*; Baygusheva, 49–53, fig. 9–11, pl. 4–7
2004 *Praemegaceros pliotarandoides*; Croitor and Kostopoulos, 155, fig. 15
2006 *Praemegaceros (Orthogonoceros) pliotarandoides*; Croitor, 98; fig. 6b
2009 *Eucladoceros orientalis pliotarandoides*; Baygusheva, 461–468; fig. 2–7
2011 *Praemegaceros (Orthogonoceros) pliotarandoides*; Croitor, 113–118; fig. 1–5

Holotype: incomplete left shed antler, Cortiglione Monferato (Italy), coll. Geological Museum of Turin.

Type locality: Cortiglione Monferato (Italy), Villafranchian/Galerian.

Age of localities of described material: Semibalki and Tsimbal are typical sites of Taman Faunal Complex (Late Villafranchian-Galerian); specimens from Taman peninsula from unknown localities are presumably late Lower Pleistocene; the antler from Mariupol is presumably late Lower Pleistocene.

Material: an incomplete skull with a right antler 388 (collection KKM) from an unknown locality on the Taman Peninsula (according to N.O. Burchak-Abramovich); skulls without antlers OP-818, OP-819 and fragment of antler (collection AMZ) from Semibalki (north-eastern Sea of Azov Region); skull without antlers 26001\1 (collection ZIN) from Tsimbal (Taman peninsula); skull fragment (collection PIN, without collection number) from Taman Peninsula; incomplete shed antler I-864 (collection MKM) from Mariupol (Zhdanov, northern Sea of Azov Region).

Description. Large deer. Width of a skull at supraorbital narrowing significantly exceeds the width of the braincase behind pedicles (Table 1). On the frontal bones at the level of top of the eye sockets there are concaves. Sagittal suture is convex, but between pedicles it is smooth. Foramen supraorbitale is large and concave. The frontal bones between pedicles are concave. Bases of pedicles are close together, and the distance between them is less than the width of the single pedicle. Lateral-medial diameter of the pedicle

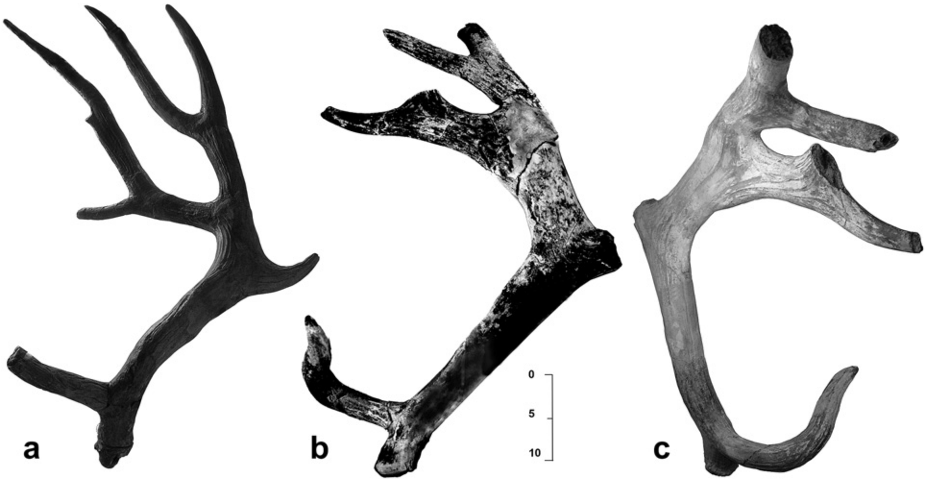

Fig. 4. Antlers of *Eucladoceros* from Northern Caucasus: *E. orientalis orientalis* from Bakinskaya (Northern Caucasus, Psekups River; Early Pleistocene, late Middle – early Late Villafranchian): (a) right antler, (PIN 4378/1): medial view; *Eucladoceros orientalis pliotarandoides* from Mariupol (exact locality unknown; Northern Sea of Azov Region; ?late Early Pleistocene): left antler (MKM-I-864): (b) lateral view, (c) anterior-medial view.

is little more than the anterio-posterior one. The divergence of pedicles is 80°. The angle of the forehead and the skullcap is 119°–120°. Post pedicle part of the skull is short. Bones of a skullcap are slightly concave. The rhomboid elevation is placed at the centre. Before the subquadrangular coronal suture on the parietal bones, there are considerable depressions. Parietal bones are laterally convex. A groove for a joint with the lower jaw is slightly sloped medially. Nuchal fossae form relief, separated by an external occipital crest (Fig. 1a–c).

Occipital protuberantia is low. The angle of convergence of the dorsal and ventral surfaces of occipital condyles is 70°. The plane of the neck makes an angle of 120° with the skullcap, and 70° with the basioccipital bone. Occipital condyles significantly jut out caudally. Hypoglossal canal opens in front of occipital condyles. Jugular process is directed downward, backward and inward. High subtriangular pharyngeal tubercles with thickening in the oral part are separated by a narrow groove. A narrow ridge extends aborally to the middle of the basioccipitale. Aboral width of basioccipital bone is 70.0 mm. The ratio of its width at the oral part to that in the aboral is 75.1%, while the same of width of narrowing to the aboral maximal part is 74.6%. Basisphenoid bone has a small groove in the center. Its border with praesphenoid is at the level of posterior-lower edges of the foramen orbitorotundum (Fig. 5b, c). Foramen ovale is large. Alisphenoideum contacts with parietale. Bone trumpet is long, with distance from the lower inner edge to the level of processus tympanohyale of 29.6 mm. It has two ridges, one directed to the temporal part, the other thin to the jugular bone. There are spinelets on the medium-sized, weakly inflated, and slightly rounded tympanic bone. Petrosus bones are slightly above the central part of basioccipitale. The canal for the hyomandibulare is elongated and covered with a thin edge of bone auditory tube.

The total length of the antler KKM 388 is about 1280.0 mm. The basal tine has a form of roughness. The dorsal tine is strongly curved outwards and downwards. It is implanted at some distance from the burr (Table 2). The crown tine has dichotomous bifurcation (Fig. 5a). The diameter of the beam after the crown tine is 58.0 × 38.0 mm. Index of flattening of tines is 0.66–0.80 (specimen KKM 388).

Comparison. The antler from Mariupol is similar with the type specimen of "*Praemegaceros*" *pliotarandoides* from Cortiglione Monferato (Italy) in the character of dorsal tine curving outwards, reduction of basal tine, and deviation of the beam. The same characteristics are present in "*Orthogonoceros verticornis*" from Aliakmon (Greece) (Croitor and Kostopoulos, 2004), but in contrast

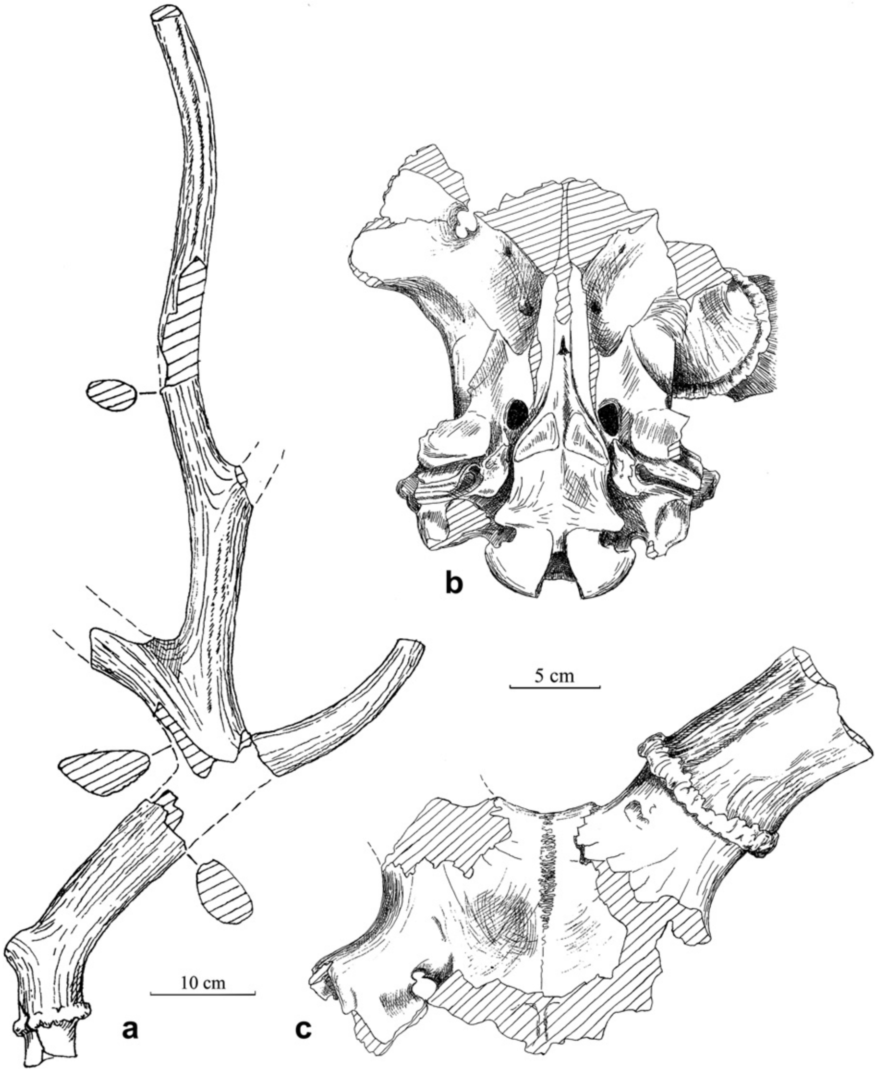

Fig. 5. *Eucladoceros orientalis pliotarandoides* from Taman peninsula (locality is unknown; ?late Early Pleistocene): (a) right antler (KKM 388): medial view; skull fragment (KKM 388): (b) ventral view; (c) rostral view. Figured by R. Croitor (2011).

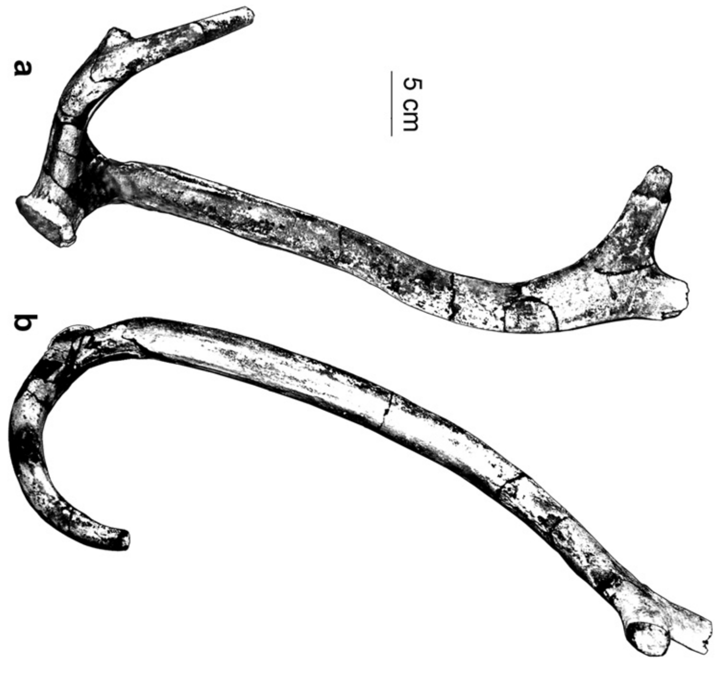

Fig. 6. Left antler of *Arvernoceros* sp. from Kushkuna (Azerbaijan; Late Pliocene, Early Villafranchian): collection NMG (without number) (a) medial view; (b) dorsal view.

to the finds from the Sea of Azov Region, the antler from Greece has is a short more evident basal tine situated near the burr.

E. o. pliotarandoides differs from *E. o. orientalis* by its greater distance from dorsal tine to crown tines, and by the more bent dorsal tine (Table 2). Bifurcation of crown tines at the specimen from Mariupol is 240.0 mm, more than double the same measurement on the antler from Psekups.

Deer antlers from Early Pleistocene localities of Sea of Azov Region differ from other forms of genus *Eucladoceros* by having noticeably bent outward and downward relatively short dorsal tine, significantly deflected laterally beam, and the presence of the dichotomy bifurcation of tines. These specimens differ from the antler from Psekups *E. o. orientalis* also in their larger size. They retain the same number and size of basal (spurious) tines, the dichotomy of the single branch diverging from the beam, and similar proportions of the beam and antler bifurcations.

Discussion. Currently, there are two main hypotheses on the systematic position of the deer genera *Eucladoceros* and *Praemegaceros*. Vislobokova (1990) considers the last as the continuation of the Asian line *Neomegaloceros* – *Orchonoceros*. *Eucladoceros* is regarded as a separate lineage of the tribe Cervini (Vislobokova, 1990, 2011). The present authors adhere to this opinion. Some researchers believe *Praemegaceros* are descendants of *Eucladoceros* (Azzaroli and Mazza, 1992; Croitor and Kostopoulos, 2004; Croitor, 2006, 2011). Antlers from Psekups, Krasnodar and Mariupol were attributed to *P.* (*Orthogonoceros*) *pliotarandoides,* and specimens from Semibalki and Taman peninsula to *P.* (*Praemegaceros*) *obscurus* (Croitor, 2005, 2011). However, deer of genera *Eucladoceros* and *Praemegaceros* have a series of significant differences. The comparison of skull parameters for different deer given by Croitor (2006) are not very convincing in relation to the proposition of genus affinity or difference. The statement of different type of dichotomy for antlers of *Eucladoceros dicranios* and "*P.*" *pliotarandoides* (Croitor and Kostopoulos, 2004) seems debatable.

Table 4
The comparison of antlers of mature and young *Arvernoceros* cf. *verestschagini* from Khapry layers, *A. verestschagini* (s. Salcia. Moldova) and *Arvernoceros* sp. from Kushkuna (Azerbaijan).

Measurements, mm	*Arvernoceros* cf. *verestschagini*								*A. verestschagini*	*Arvernoceros* sp.
	Liventsovka; coll. ROMK, AMZ						Liventsovka, all		s. Salcia; David, 1992	Kushkuna
	ad			subad					IZM 52/200	NMG, without number
	n	min–max	M	*n*	min–max	M	MAD	δ		
Burr diameter latero-medial (1)	8	59.6–71.8	65.4	9	33.6–57.8	49.2	7.16	9.35	72.0	52.0
Burr diameter anterio-posterior (2)	8	55.0–87.5	65.9	9	43.0–56.0	50.9	6.92	8.60	78.0	–
Pedicle height	6	31.0–34.0	32.3	–	27.0–30.2	28.6	2.40	3.39	–	–
Pedicle diameter latero-medial	4	48.0–58.0	52.9	–	37.8–44.2	40.7	5.39	6.26	–	–
Pedicle diameter anterio-posterior	4	48.0–54.0	52.2	–	37.4–48.0	41.9	4.33	5.78	–	–
Angle of first bifurcation, °	–	120–170	–	–	88	–	–	–	130	85
Length of first segment (length from the burr to distal end of dorsal tine base)	–	55.0–112.0	99.4	–	70.0–108.8	97.9	13.16	15.69	95.0	81.0
Length of second segment (length from the burr to distal end of dorsal tine base)	–	–	–	–	–	–	–	–	350.0	41.0
Antler's base diameter above the burr latero-medial (3)	8	47.8–59.8	55.2	8	35.2–47.6	39.4	5.98	7.60	72.0	34.4
Antler's base diameter above the burr anterio-posterior (4)	8	47.4–63.0	53.6	8	34.0–49.2	41.6	6.64	7.89	78.0	–
Length of first tine	–	–	–	–	–	–	–	–	–	(50.8)
First tine's base diameter latero-medial (5)	2	38.2; 59.0	–	1	25.0	–	–	–	90.0	–
First tine's base diameter anterio-posterior (6)	2	35.6; 46.0	–	1	41.0	–	–	–	55.0	–
Beam's diameter above the first tine lateral-medial (7)	6	48.2–61.0	57.6	3	32.4–41.0	36. 7	–	–	–	43.0
Beam's diameter above the first tine anterio-posterior (8)	6	40.8–47.2	42.2	3	34.0–41.8	37.3	–	–	–	31.0
Index of flattering of the burr (1/2)	8	0.82–1.0	0.92	9	0.78–0.99	0.94	0.04	0.06	0.92	–
Index of flattering of the antler base (3/4)	8	0.8–0.96	0.88	9	0.83–0.99	0.92	0.07	0.09	1.0	–
Index of flattering of the first tine (5/6)	2	0.6; 0.83	–	1	0.61	–	–	–	0.61	–
Index of flattering of the beam (7/8)	6	0.65–0.94	0.75	3	0.9–0.98	0.94	–	–	–	0.68

Deer antlers of *Eucladoceros* of group *dicranios-orientalis* have a clear dichotomous bifurcation, unlike deer of the genus *Praemegaceros*. The first have no intermediate middle non-bifurcated tine, and the dichotomy ramification of the tine follows the developed dorsal tine. The size of skulls of *Eucladoceros* (from Khapry layers) is less than in *Praemegaceros* (the comparison was made with specimens of *P. verticornis* from Kolkotova Balka, Tiraspol; collections of GGM and MGRI). The proportions of the skull differ in these types of deer. Latitude measurements of *Praemegaceros* are larger, but the length is less. Thus, the skull post pedicle length of the deer *Eucladoceros* from Liventsovka is on average 79.8 mm ($n = 4$), and in *Praemegaceros* 72.7 mm ($n = 3$) with a greater width. The ratio of the width of the skull behind pedicles to post pedicle length is 150.9 (*Eucladoceros*) and 196.5 (*Praemegaceros*). The width of supraorbital narrowing to the width behind pedicles is 137.2 on average ($n = 5$) and 119.6 ($n = 3$), respectively. The ratio of the width of the ventral notch to the width of occipital restriction in front of the occipital ridges is 0.148 ($n = 4$) and 0.196 ($n = 3$), respectively. The ratio of height to the neck to mastoid width is 67.6 and 59.8 (at the skull from Psekups 42.9). Basioccipitale is noticeably wider at *Eucladoceros* at the narrowing and aboral parts in comparison with *Praemegaceros*. The ratio of its oral width to the aboral one is 74.0 ($n = 4$) and 66.8 ($n = 3$), but the width of the narrowing to the aboral one is 79.2 ($n = 4$) and 65.4 ($n = 3$). Occipital condyle relative to the width of the occipital bone is greater in *Eucladoceros* 66.7 ($n = 3$) and 56.1 ($n = 3$) in *Praemegaceros*. The angle of pedicle divergence is less in *Eucladoceros* (average 80°), than in *Praemegaceros* (average 90°). The form of pedicles is the same: the transverse width is on average greater than anteroposterior length (based on the *Eucladoceros* material from Liventsovka). Later representatives of *Eucladoceros* have the similar shape of the very large dorsal tine with the presence of a reduced basal one.

The material described here traces the gradual transformation of antlers of *Eucladoceros* ex gr. *dicranios-orientalis* from Middle Villafranchian to Late Villafranchian forms. They become larger, with less flattening of beam and tines, increasing height of divergence of the dorsal tine, increasing of distance between the proximal and crown tines, reduction of distal tine and total elongation of antlers, under the preservation of the dichotomous bifurcation.

The basal tine is significantly reduced, becoming a button-like vestige (subbasal tine according to Croitor, 2006). A similar feature is observed in young individuals of *Eucladoceros* of the Khapry Complex. Increased bending of dorsal tine and decreased its ramification. Significant bending of the dorsal tine in *E. orientalis* resembles the same at *Praemegaceros*. In the latter, however, this tine was longer and more curved (Abbazzi, 2004). This similarity in the structure of antlers in both deer lineages may be the result of parallel evolution during landscape change on the transition between Villafranchian and Galerian.

Tribe Megacerini Viret, 1961

Genus *Arvernoceros* Heintz, 1970

Arvernoceros sp.

Locality: Kushkuna, Azerbaijan

Age of the locality: Upper Pliocene, Lower Villafranchian.

Material: The shed left antler of a young animal (without a collection number, collection of the National Museum of Georgia).

Description and comparison. The antler is characterized by a round cross section beam, lacking other ramifications in the beam on a great distance from the first tine (Fig. 6). Beam is straight, and in the distal quarter it bends upward. A distal part of the antler is flattened and bifurcated in two tines, which are located in one plane. At the level of the first tine, the beam deviates back and laterally. The first tine is located at a relatively short distance from the burr, direct forward, and curved upwards and outwards at the end (Table 4). It has a small additional internal tine. The basal tine is rounded at the base. The first tine forms close to a 90° angle with the beam. At a distance of 40 cm after the divergence from the fist tine, the beam is somewhat flattened. The distance from the middle of burr to bifurcation of distal crown tines exceeds 180 cm. One of these terminal tines is directed forward and outward, and the second upward and sideways. The surface of the antler is almost smooth.

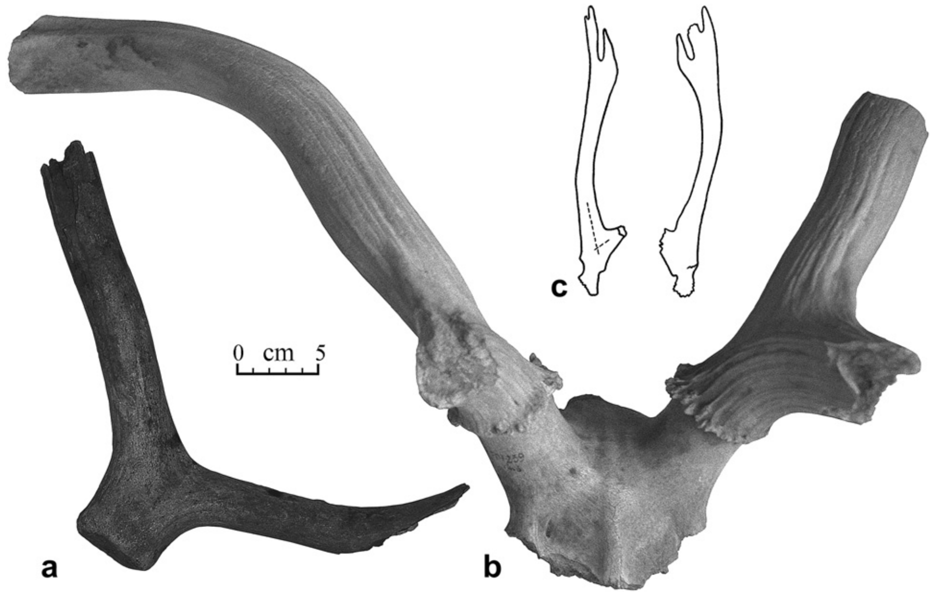

Fig. 7. *Arvernoceros* cf. *verestschagini* from Liventsovka sand pit (North-Eastern Sea of Azov Region; Early Pleistocene, Middle Villafranchian): (a) the fragment of the antler (AMZ OP-1422): medial view; (b) the part of the skull with the fragments of antlers (AMZ OP-1425 (RGU – 239)): rostral view; (c) the outline of left antler (GIN, No. 301–12), locality Morskaya (by Alexeeva, 1977).

As this specimen is from a young individual, it is difficult to make the species determination. The size and features of this finding are similar to those of Early Villafranchian *A. ardei* (Croizet et Jobert) from Etouaires (France) and Villarroy (Spain) and antlers of young *Arvernoceros* cf. *verestchagini* of Khapry layers of Sea of Azov Region.

Remarks. The antler is known from the site Kushkuna (Azerbaijan) found together with the remains of rodents, and molluscs of Middle Akchagylian. Paleomagnetic and biostratigraphic data of the layers relate them to the second half of the former Late Pliocene (=Piacenzian), Early Villanyian, and zone MN 16b (Tesakov, 2004).

Arvernoceros cf. *verestschagini* David 1992

1948 *Cervus* sp.; Gromov, 45
1971 *Arvernoceros* sp.; Baygusheva, 23
1994, *Arvernoceros* sp.; Baygusheva, 246
1990 *Arvernoceros* sp.; Vislobokova, 186
2004 *Arvernoceros* sp.; Croitor and Kostopoulos, 139.

Type locality: Salcia (Moldova); Early Pleistocene.

Localities of described material: Liventsovka, Khapry, Rostov Region, Russia, Khapry layers.

Age of the localities: Lower Pleistocene, Middle Villafranchian.

Material: skull fragments with antlers (5 specimens), 19 fragmentary antlers, 7 lower jaws, 16 limb bones; collections of AMZ, ROMK, PIN, GIN.

Description. The main characteristics of the skull of a deer are the following: post pedicle part of the skull is long, the ratio of width to cranial to post pedicle length is 1.38; frontal surface on each side of the sagittal suture behind orbits is concave (this feature varies, probably depending on the antlers' size); relatively small occipital condyles; frontal bones between pedicles are flat; supraorbital channel is strongly narrowed upwards and widened downwards; coronal suture is subtriangular; orbits jut out; temporal crest is massive; supraorbital narrowing is weak; the angle of frontal and post pedicle planes is 98–102°; the angle between the parietal and occipital bones is 130°; large and elongated oval foramen, parietal foramen is small, temporal foramen is large; bone external acoustic meatus is directed dorso-laterally and slightly lopsided back, pharyngeal tubercles are large, and longitudinally elongated. Pedicles are relatively long, their length ranges. Angle of pedicles' divergence is 70–80°, and the distance between them does not exceed the horizontal diameter of the single pedicle (Fig. 7). The burr is well developed, elliptical in cross section.

Antlers are characterized by rounded cross section beam, without any ramifications at a great distance above the first tine (Table 4, 5). The beam can be straight or curved. Angle of divergence of pedicles is 85°. At the level of the first tine, the beam extends posterior and laterally. The first tine is located at some distance from the burr, directed forward and is curved upward at the end. It is flattened at the base in adult individuals, but rounded at young ones. On large specimens, there is an additional process on the basal tine. The first tine forms with the beam an angle close to 90° (young), more obtuse in adults, about 110°. On antlers of young animals there is a weak ridge between the first process and the beam. The distance from the first tine to the palmation is more than 390 cm. There are no fully preserved antlers with palmation in the collection. However, according to the picture of an adult individual antler from the Morskaya locality (Alexeeva, 1977) there are three terminal tines directed forward (Fig. 7c). The surface of the horn is weakly striated, and in young forms is almost smooth.

The lower edge of the lower jaw is convex. The angle of the ascending branch to the body of the jaw is 135°. Teeth p4 are weakly molarized, representing the third molarization stage (Heintz, 1970). The anteroexternal plicas on molars are not pronounced.

Table 5
Antlers' measurements of mature and young *Arvernoceros* cf. *verestschagini* from Khapry layers. Data in parenthesis are approximate.

Measurements, mm	L-448	L-1073	L-1265	L-1491	L-1640	L-1784	L-882	Kh-747	GIN-300/12	L-1333	L-758	MCH–1760	L-1590	L-1662	L-147	L-1724	L-1824	L-115
Burr diameter latero-medial	65.4	59.6	63.0	63.2	(61)	(55)	(52)	–	–	(51)	49.0	51.0	48.8	54.0	63.0	54.0	(43)	33.6
Burr diameter anterio-posterior	70.0	60.8	67.8	63.2	(69)	(63)	(53)	–	–	(56)	54.2	52.0	49.2	55.4	67.0	57.8	(43)	42.2
Pedicle height	–	–	–	–	–	–	30.2	–	–	–	29.4	27.0	–	–	32.0	28.0	22.2	–
Pedicle diameter latero-medial	–	–	–	–	–	53.6	48.0	–	50.0	–	37.4	38.0	–	–	48.0	47.2	39.2	–
Pedicle diameter anterio-posterior	–	–	–	–	–	54.0	44.2	–	38.4	–	39.4	39.0	–	–	48.0	43.4	37.8	–
Length of first segment (length from the burr to distal end of dorsal tine base)	108.0	111.2	112.0	106.4	107.0	108.2	128.4	113.0	–	113.2	92.2	91.4	107.0	85.0	–	84.0	77.6	70.0
Antler's base diameter above the burr latero-medial	47.8	57.6	56.4	51.2	47.4	50.0	44.2	32.0	53.0	47.6	42.0	38.6	35.2	44.0	53.0	45.2	(41)	34.2
Antler's base diameter above the burr anterio-posterior	51.6	53.8	59.2	59.8	59.0	58.0	43.4	41.6	53.0	49.2	44.6	44.4	34.0	49.0	58.0	54.2	(41)	41.2

Comparison. The large size and the form of antlers bring together the form of this deer with *A. ardei* from the early Villafranchian localities Etouaires and Villarroya. Deer from the Liventsovka sand pit differ from the type species by greater transverse pedicle width at the same its height at adult individuals and some smaller at young ones, larger burr; and larger angle of pedicles' divergence (Heintz, 1970; Baygusheva, 1994). Teeth of *Arvernoceros* from Khapry layers on average are larger than those in deer from Etouaires and Villarroya, but lie within the variability of this species or slightly exceed them.

The close geological age and geographical location, and the similar size suggest a possible relationship between *Arvernoceros* from the Khapry layers and *A. verestschagini* from Lower Pleistocene deposits near Salcia in Moldavia (David, 1992). However, the antlers of Khapry differ from the type specimen of the Moldavian deer by having a more slender beam over the burr, smaller height of a thinner first tine divergence, and larger angle of the first bifurcation.

3. Conclusions

In the Pleistocene of the Sea of Azov region, representatives of the genera *Eucladoceros* and *Arvernoceros* were most numerous forms of large deer. In Eastern Europe and adjacent territories, representatives of the first genus have existed since the Late Pliocene. A fragment of the skull and the antler is known from Early Villafranchian locality of Kvabebi in Georgia (Vekua, 1972). In the subsequent Khapry, Psekups and Taman Faunal complexes of Middle-Late Villafranchian, they were the index forms of large mammals. The evolutionary line of these deer reveals, for southern Eastern Europe: *Eucladoceros dicranios tanaitensis – E. o. orientalis – E. o. pliotarandoides*. Probably, at this time in this territory, the first representatives of the genus *Praemegaceros* already existed (Vislobokova, 1990; Croitor, 2005). Throughout the evolution *Eucladoceros* ex gr. *dicranios-orientalis* became larger, with less flattening of beam and tines and a reduction of basal tine, increased height of divergence of the dorsal tine, increased distance between the basal and dichotomy bifurcated crown tines, and total elongation of antlers.

Arvernoceros in Eastern Europe began to exist in the Early Villafranchian, as shown by the findings of this deer from Kvabebi (Georgia) (Vekua, 1972) and Kushkuna (Azerbaijan). These sites of zone MN 16 are close in age to locations of Western Europe at Etouaires and Vialette (France), and Villarroya (Spain), where *A. ardei* are known (Heintz, 1970; Vislobokova, 1990). Representatives of this kind existed in Eastern Europe to the end of Early Pleistocene. In the Sea of Azov region, they were typical representatives of the Middle Villafranchian Khapry Faunistic complex. Among all the finds of fragments of skulls and antlers of deer in the Khapry deposits, 12.3% belong to *Arvernoceros*. *A. verestschagini* was described from the early Lower Pleistocene of Moldova. From the type locality of Psekups, complex remains of *Arvernoceros* are unknown. However, this form of deer was typical for this time period in Eastern Europe and adjacent territories. The locality of Dmanisi (Georgia) has Cervidae cf. *arvernoceros* (Vekua, 1995), and *Arvernoceros* sp. are present in the Romanian location of Fantana lui Mitinan (Croitor, 2005). From numerous localities of the Taman complex, remains of *Arvernoceros* are also not defined. However, these deer are known from other sites of similar age from Europe: *Arvernoceros* sp. from Chishmikioy (Moldova), and *Arvernoceros* cf. *verestchagini* from Apollonia-1 (Greece) (Croitor and Kostopoulos, 2004; Croitor, 2005). During the Pleistocene, the evolution of the genus was directed to increasing the total size and complexity of the structure of the first tine. All these changes took place against the background of gradual aridification of the climate and expansion of the steppe type plant communities.

The changing of deer subspecies took place in parallel with modification of another index subspecies, the southern elephant *Archidiskodon*. In the following Middle Pleistocene Tiraspol Faunal complex, the deer *Praemegaceros ex gr. obscurus-verticornis* prevailed, which coexisted with *Mammuthus trogontherii*.

Acknowledgements

We thank Dr. I.A. Vislobokova for a discussion of the material, as well as Dr. R. Croitor for presenting their point of view on the material. We are grateful to Dr. J. van der Made and Dr. J. de Vos for important remarks to the manuscript.

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Abbreviations

AMZ: Azov Museum Reserve, Azov, Russia
GGM: State Geological Museum, Moscow, Russia
GIN: Geological Institute of Russian Academy of sciences, Moscow, Russia
IZM: Institute of Zoology of Moldova, Chisinau, Moldova
MGRI: Moscow State Geological Research University, Moscow, Russia
MKM: Mariupol Local Museum, Mariupol, Ukraine
NMG –: National Museum of Georgia, Tbilisi, Georgia
PIN: Paleontological Museum of Russian Academy of sciences, Moscow, Russia.
ROMK: Rostov-on-Don Regional Museum, Rostov-on-Don, Russia
ZIN: Zoological Institute of Russian Academy of sciences, St.-Petersburg, Russia
KKM: Krasnodar Local Museum, Krasnodar, Russia