Cover Design
Jerzy ŚWIECIMSKI

The rhiniceros on the cover presents a nearly complete specimen of the Pleistocene *Coelodonta antiquitatis*, excaved in the layers of ozocerite in Starunia (Eastern Carpathians), 1929. This unique exhibit is shown in the Natural History Museum (Institute of Systematics and Evolution of Animals), Cracow.

Megaceroides obscurus (AZZAROLI, 1953) (Mammalia, Cervidae) from early Pleistocene sites of Eastern Moldova

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Abstract. Remains of the large-sized deer *Megaceroides obscurus* have been recognised in mammal assemblages from early Pleistocene sediments of Moldova. The species *M. obscurus* is fairly well represented in the early Pleistocene localities of Western Europe (e.g. Italy and England) referred to the Late Villafranchian (Farneta faunal unit). It is a direct ancestor of the well-known and widespread species *M. verticornis* which is characteristic of the Galerian faunal assemblages of the late early and middle Pleistocene. The remains from Moldova add to the knowledge of the early phase of dispersal of the genus *Megaceroides* in the European regions.

Key-words: Cervidae, *Megaceroides*, Systematics, Moldovan Republic, Early Pleistocene.

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I. INTRODUCTION

This paper is the first report on the occurrence of the large-sized deer *Megaceroides obscurus* (AZZAROLI, 1953) from the early Pleistocene sediments of localities in the Moldovan Republic. *M. obscurus* is so far the oldest and most primitive species of the genus *Megaceroides*; its occurrence characterises European assemblages of the upper part of the Late Villafranchian (according to the biochronological scheme used in the West of Europe – AZZAROLI 1977; TORRE et al. 1992; MASINI et al. 1995) and of the Odessan complex (according to the scheme used in the East of Europe, NIKIFOROVA et al. 1982, MARKOVA 1990).

The large-sized cervids of the tribe Megalocerini VIRET, 1961, constituted an important element in the European faunas starting from the early Pleistocene. These deer, first united in the genus *Megaceros* OWEN, 1844, later emended into *Megaloceros* BROOKES, 1828 (LISTER 1987), actually belong to distinct phylogenetic lineages. On the basis of morphological characters of skull and antlers AZZAROLI (1952) recognised the existence of two groups, whose formal status he did not give: the *Megaceros verticornis* (DAWKINS, 1872) group characterised by a convex or flat forehead, and antlers with the basal tine rounded in cross-section and the second tine set in a dorsal position, and the *Megaceros giganteus* (BLUMENBACH, 1803)group with concave foreheads and a markedly flattened first tine. Subsequently, AMBROSETTI (1967) referred the groups recognised by AZZAROLI (1952) to *Megaceros* (*Megaceroides*) and *M.* (*Megaceros*), respectively. The systematic definition

of Megalocerini has been dealt with by many other authors, to whom the reader is referred for further details (KAHLKE 1956, 1965, 1969; RADULESCO and SAMSON 1967; GERAADS 1986; LISTER 1987; HADJOUIS 1990; VISLOBOKOVA and CHANGKANG 1990). Recently, AZZAROLI and MAZZA (1992, 1993) have proposed to raise *Megaceroides* JOLEAUD, 1914, to generic rank in as much as it had an independent origin from *Megaloceros*.

Megaceroides includes closely related species which are well represented in European and Middle Eastern assemblages of the early and middle Pleistocene and in the late Pleistocene of North Africa. Within this genus, two phyletic lines are recognisable: the line connecting the species *M. obscurus* and *M. verticornis*, and that of *M. Solilhacus* (ROBERT, 1829). The second group comprises also *M. Dawkinsi* (NEWTON, 1882), the species endemic to England, characterised by a significant reduction of size (AZZAROLI 1953), but close to *M. solilhacus* in antler morphology. These two lineages seem to have already been separated since the early Pleistocene, as suggested by the occurrence of a form similar to *M. solilhacus* in Spain (Venta Micena, MENENDEZ 1987) and of *M. obscurus* in Italy, England (ABBAZZI 1995) and Moldova (present paper). At present, the mode in and tempo at which the two lines separated are unclear. Further, though the megaceroid from Venta Micena agrees with *M. solilhacus* in the morphology of the proximal part of the antler (i.e. lack of basal tines), it differs from the material recovered from the type locality (surroundings of Solilhac, ROBERT 1829; MOULLADE 1886; cf. AZZAROLI 1979) and from other European sites (e.g. Isernia La Pineta, ABBAZZI and MASINI 1997), in its slender limb bones, distinctly smaller braincase, and in some plesiomorphic characters, such as the more elongated cranial roof and the differently directed pedicles (for comparison see the skull of *M. solilhacus* from Blanzac, AZZAROLI 1979). These differences evidence that systematic revision of this material is needed.

M. algericus (LYDEKKER, 1890), the type species of the genus according to AZZAROLI and MAZZA (1993), is a younger form of *Megaceroides* limited to North Africa (Algeria, Morocco, JOLEAUD 1916; HADJOUIS 1990). It may have been an offshoot of *M. verticornis* or an independent, though closely related, lineage.

The species referred to the genus *Megaceroides* share a general structure of antlers, which show a proximal part oriented more or less horizontally, and an approximately vertical distal part. The posterior tine is inserted in the place of marked change in the orientation of the beam. Conversely, the development and occurrence/absence of the basal tines, namely, spurious and outer tines according to AZZAROLI and MAZZA (1992, 1993), show a greater variability and therefore they are the
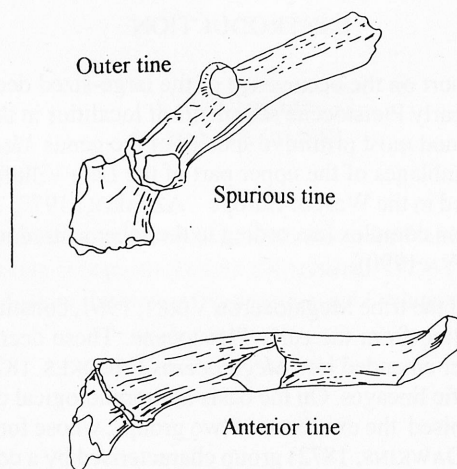

Fig. 1. Terminology of tines in the proximal subhorizontal part of antler of *Megaceroides*. The extremes in the morphological variability of this part of the beam are shown. a) *M. obscurus*, lectotype from Mundesley, East Anglia, Cromer Forest Bed Formation; b) *M. solilhacus*, lectotype from Solilhac (after AZZAROLI 1979). Left antlers in anterior view. The measure is 10 cm.

main diagnostic characters in separating particular species (Fig. 1). As a matter of fact, the spurious tine is well developed in the archaic forms (*M. obscurus*), while it is in general reduced to a knob or even absent in the more advanced species (*M. verticornis*). The outer tine undergoes a reduction mainly in the lineage of *M. solilhacus* where it may disappear. Moreover, the beams tend to become shorter and to lie almost horizontally in the more derived forms (ABBAZZI and MASINI 1997). The regression of the basal tines in *Megaceroides* was already noted by KAHLKE (1956), who however did not describe the forms characterised by different stages of development as distinct taxa, but as morphotypes within the species *verticornis*. As regards the skull, the primitive forms of *Megaceroides*, like *M. obscurus*, have their forehead slightly concave.

Megaceroides seems to have originated from the genus *Eucladoceros* as suggested by the occurrence of intermediate forms between the two genera. An antlered skull of a large juvenile deer is stored the Geological and Palaeontological Museum of the University of Florence. This specimen, coming from early Pleistocene sediments of the Petrignano locality (Val di Chiana, Farneta faunal unit), has been referred by AZZAROLI and MAZZA (1992) to *E. ctenoides* (NESTI, 1879). It is characterised by the outer tine departing dorsally from the beam to bend downwards, and by a possible posterior tine where the beam tends upwards (see fig. 8, n.1 in AZZAROLI and MAZZA 1992). These characters, which represent apomorphies, indicate that the specimen is very close to *Megaceroides obscurus* and may be considered as transitional between the two genera. Plesiomorphic features in the skull, such as concave foreheads, large ethmoidal fissures and preorbital pits, are common to *M. obscurus* and *Eucladoceros*.

Another intermediate form has been recovered from the locality Rotbav-Silvestru in Romania (early Pleistocene) and referred to the new genus and species *Allocaenelaphus arambourgi* by RADULESCO and SAMSON (1967) to stress its uncertain systematic position. As a matter of fact, the straight antlers and the insertion of the anterior tine in the same plane of the second tine recall *Eucladoceros*, while the morphology and position of the basal tines, and the stoutness of the postcranial remains render this form closer to *Megaceroides*, to which it is at present referred (GERAADS 1986). In detail, excluding the occurrence of the anterior tine, which may be considered an anomaly or a re-entry into the morphological variability of the species, the proximal part of the antlers of *M. "arambourgi"* RADULESCO & SAMSON, 1967) is very similar to that of *M. obscurus*, suggesting their being conspecific.

II. THE SPECIES *MEGACEROIDES OBSCURUS*

The species *Megaceroides obscurus* was described under the name *"Cervus" obscurus* by AZZAROLI (1953) on the basis of some antlers found in the Cromer Forest-bed formation (Mundesley, Trimingham and Overstrand), which appeared of doubtful systematic position because of their morphology somewhat intermediate between *Eucladoceros* and *Megaceroides*. In subsequent works, this form was referred to the genus *Megaceroides* and considered a synonym of *M. verticornis* (AZZAROLI 1979, 1994; GERAADS 1986; AZZAROLI and MAZZA 1993); the morphological features of *M. obscurus*, such as the well developed spurious tine, were in fact believed to be anomalies within the variability of the species *verticornis*. On the contrary, the finds from the Central Italian localities Pietrafitta and Cava Liberatori show that this feature is widespread among the late Villa-

franchian megaceroids, where it is always accompanied by a very long outer tine positioned dorsally and by moderately diverging beams (about 90°). The consistent association of these characters suggests that these specimens belong to a distinct taxon.

The most representative sample of the species *obscurus* has been found at Pietrafitta. These fossils come from a single horizon of lignite within a fluvio-lacustrine succession, and are associated with taxa characteristic of the Farneta faunal unit e.g. *Archidiskodon meridionalis vestinus* AZZAROLI, 1997, *Leptobos* aff. *Vallisarni* MERLA, 1949, *Pseudodama farnetesis* AZZAROLI, 1992, *Microtus (Allophaiomys)* cf. *ruffoi* PASA, 1947; cf. MASINI et al. 1995). It is only at this site that an antlered skull and postcranial bones have been found anatomically joined. These remains are of larger size and more sturdy than those of the Late Villafranchian *Eucladoceros*. The large-deer from Pietrafitta, previously referred by AZZAROLI and MAZZA (1992, 1993) to the new species *M. Boldrinii* AZZAROLI and MAZZA, 1992, is represented also by several fragmentary antlers and some isolated teeth and postcranial remains. At Cava Liberatori, where remains of a faunal assemblage referred to the Farneta faunal unit have been recovered (*Archidiskodon meridionalis vestinus* AZZAROLI, *Leptobos* aff. *vallisarni*, *Pseudodama farnetesis* AZZAROLI, *Equus* aff. *Stehlini* AZZAROLI, *Equus stenonis* COCCHI, 1867), an antlered skull of *M. obscurus* has also been found (ABBAZZI 1995). At Selvella (Val di Chiana, Central Italy, DE GIULI 1987) only some postcranial remains of a large-sized deer, previously referred to *Eucladoceros* cf. *dicranios* (NESTI, 1879) (DE GIULI 1987; AZZAROLI and MAZZA 1993), have been recovered. This locality is close in age to Cava Liberatori, as suggested by the taxonomic composition of the fauna. The deer from Selvella may be referred to *M. obscurus,* as indicated by its size larger than that of *Eucladoceros* and by the biochronological position of the locality.

More difficulties arise when *M. obscurus* occurs in the same locality, together with both *Eucladoceros* and other species of *Megaceroides*, as for instance in the sediments of the Cromer Forestbed Formation, which contain different fossiliferous horizons mainly of early and early middle Pleistocene age (GIBBARD et al. 1991; LISTER 1993). In this case it is difficult to distinguish, at least, between the postcranial remains of *M. verticornis* and *M. obscurus*, because no great morphological differences can readily be perceived between them.

III. THE LOCALITIES

Stratigraphical   and   biochronological   setting

The fossil remains of *M. obscurus* described in the present paper were collected from alluvial deposits of the ancient Nistru (Dnestr) exposed in the following sites of Eastern Moldova (Fig. 2): Salcia, Cobusca Veche (Anenii Noi district), Firladeni, Ursoaia (=Tanatari, Canusheni district). The most interesting site from the geological and paleontological viewpoint is the gravel-sand quarry near the village of Salcia. The alluvial deposits of this quarry consist of two sequences. The lower sequence, approximately 3-4 m thick, is mostly composed of yellow-grey cross-bedded sands with gravel lenses and underlain by Upper Sarmatian clays. The remains of the following mammals have been found in these deposits: *Desmana thermalis* KORMOS, 1930, *Proochotona eximia* CHOM., *Citellus nogaici* TOP., *Spalax minor* TOP., *Allocricetus* cf. *ehiki* SCHAUB, 1930, *Villanyia petenyii* MEHELY, 1914, *V. fejervaryi* KORMOS, 1934, *Prolagurus arankae* KRETZOI, 1954, *P. pannonicus* KORMOS, 1930, *Promimomys moldavicus* KORM., *Mimomys reidi* HINTON, 1910, *M. intermedius* NEWTON, 1881, *M. hintoni* KRETZOI, 1941, *Allophaiomys pliocaenicus* KORMOS, 1932, *Vulpes* sp., *Crocuta* (?) sp., *Felis (Lynx) issiodorensis* CR. et JOI., *Felis* sp., *Anancus* sp., *Archidiskodon gromovi* ALESKEEVA and GARRUT, 1965, *Archidiskodon* sp., *Hipparion* sp., *Equus* cf. *livenzovensis* BAJG., *Equus* ex. gr. *stenonis*, *Dicerorhinus* cf. *etruscus* (FALCONER, 1868), *Elasmotherium* sp., *Paracamelus gigas* SCHLOSSER, 1924, *Procapra* sp., *Bison* sp. (DAVID *et al.* 1988; DAVID
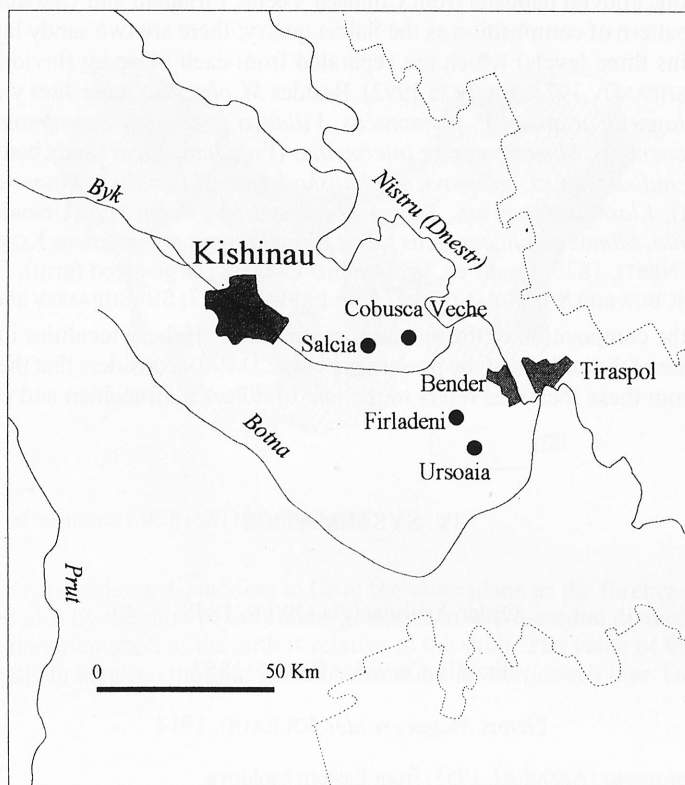
Fig. 2. Location map of the Moldovan sites considered in the text.

1989; SHUSHPANOV 1989; DAVID and OBADA 1993). The lower alluvial sequence is overlain by sandy green-gray clays, 0.5 m thick; this bed is void of fossils.

The upper alluvial deposits, about 4-5 m thick, are composed of yellow-grey cross-bedded sands with gravel lenses in the basal part. The majority of fossils, including the material of the deer under study are collected from this very part of the sequence, and belong to the following taxa: *Proochotona eximia*, *Trischizolagus dumitrescuae* RADULESCO and SAMSON, *Citellus* sp., *Pliopygeretmus* cf. *brachydens* TOP. et SCOR., *Spalax minor*, *Cricetus cricetus* LINNAEUS, 1758, *Cricetulus* sp., *Dolomys milleri* NEHRING, 1898, *Clethrionomys* sp., *Villanyia fejervaryi*, *Prolagurus arankae*, *P. pannonicus*, *Mimomys reidi*, *M. intermedius*, *M. pusillus* MEHELY, 1914, *Allophaiomys pliocaenicus*, *Canis* cf. *etruscus* F. MAJ., *Homotherium* sp., *Felis (Lynx) issiodorensis*, *Archidiskodon meridionalis meridionalis* AZZAROLI, 1977, *Archidiskodon* sp., *Palaeoloxodon* sp., *Hipparion* sp., *Equus* ex. gr. *stenonis*, *Dicerorhinus* cf. *etruscus* (FALC.), *Elasmotherium* cf. *peii* CHOW MINCH., *Paracamelus gigas*, *Arvernoceros verestchagini* DAVID, *Eucladoceros* sp., *Megaceroides verticornis* (DAVID et al. 1988; DAVID 1989; SHUSHPANOV 1989; DAVID and OBADA 1993).

The faunal composition of the remains from the alluvial sequences mentioned above is heterogeneous and includes taxa characteristic of different biochronological units from the middle Pliocene to middle Pleistocene (RADULESCO and SAMSON 1985; VISLOBOKOVA et al. 1995). The occurrence of *M. obscurus* agrees with that of *E. stenonis* and *M. (Allophaiomys) pliocaenicus*, pointing to the presence of an early Pleistocene faunal horizon.

The fossiliferous alluvial deposits from Cobusca Veche, Firladeni and Ursoaia, have approximately the same pattern of composition as the Salcia quarry: there are two sandy layers (the quarry of Ursoaia contains three levels) which are separated from each other by fluvio-lacustrine clays (HUBCA and SHUSHPANOV 1973; BILINCIS 1992). Besides *M. obscurus* these sites yielded: *Proochotona eximia, Prolagurus arankae, P. pannonicus, Villanya fejervaryi, Promimomys moldavicus, Mimomys* cf. *pliocaenicus, Mimomys* ex gr. *intermedius* (Firladeni, upper sandy bed), *Allophaiomys pliocaenicus, Archidiskodon* cf. *gromovi, Archidiskodon meridionalis , Equus* ex. gr. *stenonis* (large-sized form), *Elasmotherium* sp., *Sus* sp., *Leptobos* sp., *Bison* sp., (Ursoaia, upper level); *Proochotona eximia, Mimomys pliocaenicus* MAJ., *Allophaiomys pliocaenicus* KORM., *Archidiskodon meridionalis* NESTI, 1825, *Equus* ex. gr. *stenonis* COCCHI (large-sized form), *Dicerorhinus* cf. *etruscus* FALC. (HUBCA and SHUSHPANOV 1973, ALEXEEVA 1977; SHUSHPANOV and DAVID 1986).

Neither does the composition of the mammal assemblages of these localities indicate a unique faunal horizon. One of the authors of the present paper (A. DAVID) considers that the greatest part of the theriofauna from these localities refers to the late Middle Villafranchian and early Late Villafranchian.

IV. SYSTEMATICS

Order Artiodactyla OWEN, 1848

Family Cervidae BAIRD, 1857

Genus *Megaceroides* JOLEAUD, 1914

Megaceroides obscurus (AZZAROLI, 1953) from Eastern Moldova

M a t e r i a l. The material is stored at the Department of Paleozoology of the Institute of Zoology, Academy of Sciences of Moldova, in Kishinau.

Skulls: a forehead with basal parts of antlers (Salcia 52/1349); a braincase without antlers (Firladeni, 53/1).

Antlers: a shed right antler with a detached distal fragment (Ursoaia, 1990); a shed right antler with its spurious tine and distal portion damaged (Salcia, 21.VI.1991); basal fragments of antlers inserted in the pedicles (Salcia: 52/391, 52/393, 52/453, 52/612, 52/397, 52/1309, 52/396, 52/403, 52/399; Cobusca: 15/2.

Postcranial bones: distal fragments of humerus (Salcia: 52/503, 52/358, 52/1396, 52/1328); proximal fragments of radius (Salcia: 52/341, 52/1089, 52/504); proximal fragments of metacarpus (Salcia: 52/368, 52/742, 52/362; 52/1325, 52/1326); distal fragment of tibia (Salcia: 52/267, 52/264, 52/359); proximal fragments of metatarsus (Salcia: 52/138, 52/739, 52/1339, 52/268); distal fragments of metatarsus (52/365, 52/294); a complete metatarsus 52/273.

C o m p a r a t i v e m a t e r i a l. Remains of *Eucladoceros dicranios-ctenoides* from late Pliocene-early Pleistocene localities in Italy (stored at the Geological and Paleontological Museum of Florence); *Megaceroides verticornis* from Tiraspolian gravel (Moldova, early Middle Pleistocene, stored at the Institute of Zoology of Kishinau), Süssenborn and Voigtstedt (Germany, early middle Pleistocene, stored at the Institut für Geowissenschaften Bereich Quartärpaläontologie of Weimar), and from the Cromer Forest-bed Formation (early and early middle Pleistocene, stored at the Natural History Museum of London), were also used for comparative study.

D e s c r i p t i o n. Skull: Sample No 52/1349 bears fragments of antlers (Fig. 3). The posterior part of the left pedicle is damaged. The frontal bones are concave, the frontal suture forms a distinct bony ridge. The pedicles are strong, directed upwards and sidewards, diverging at an angle of about 90°. In this character they differ from *M. verticornis*, whose pedicles are considerably de-
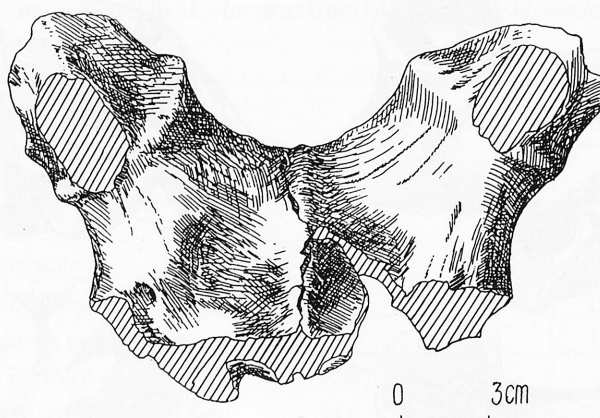
Fig. 3. Frontal view of fragmentary skull (52/1349) from Salcia.

flected backwards and sidewards, tending to lie in the same plane as the forehead. This difference can be expressed also by the ratio of the antero-posterior to latero-medial diameter of the pedicles which indicates the orientation of the antlers relative to the skull. The value of the index in *M. obscurus* is intermediate between those of *Eucladoceros* and *M. verticornis* (see Table I).

Table I

Comparison of the indices of compression of pedicles in *Megaceroides obscurus*, *M. verticornis* and *Eucladoceros*. For further explanation see text

Taxa	Range	n	Mean
M. obscurus, Moldova	88.5-100.0	10	95.1
M. obscurus, Italy and Cromer Forest Bed Formation	90.0-96.9	3	93.3
M. verticornis, Tiraspol	74.8-83.8	8	79.5
M. verticornis, Süssenborn	66.4-91.3	7	81.55
M. verticornis, Cromer Forest Bed Formation	67.5-93.6	7	78.76
Eucladoceros cf. *dicranios*, Rostov (cf. BAIGUSHEVA 1994)	102.3-103.7	2*	103

* – left and right pedicles belonging to the same individual.

The bases of pedicles in *M. obscurus* from Salcia are bordered by faint bony ridges, the character widespread in both *Eucladoceros* and *Megaceroides verticornis*.

Braincase No 53/1 from Firladeni is partially damaged (Fig. 4). The morphology of the pedicles and forehead of the skull is the same as in the frontal fragment from Salcia and the neurocranium is elongated. This specimen shows slightly prominent condyles, which in ventral view form a narrow groove (Fig. 4d). This feature can be observed in the skull of *M. obscurus* from Pietrafitta and in that of *M. verticornis* from the Italian locality Borgonuovo (AZZAROLI 1976; early middle Pleistocene,
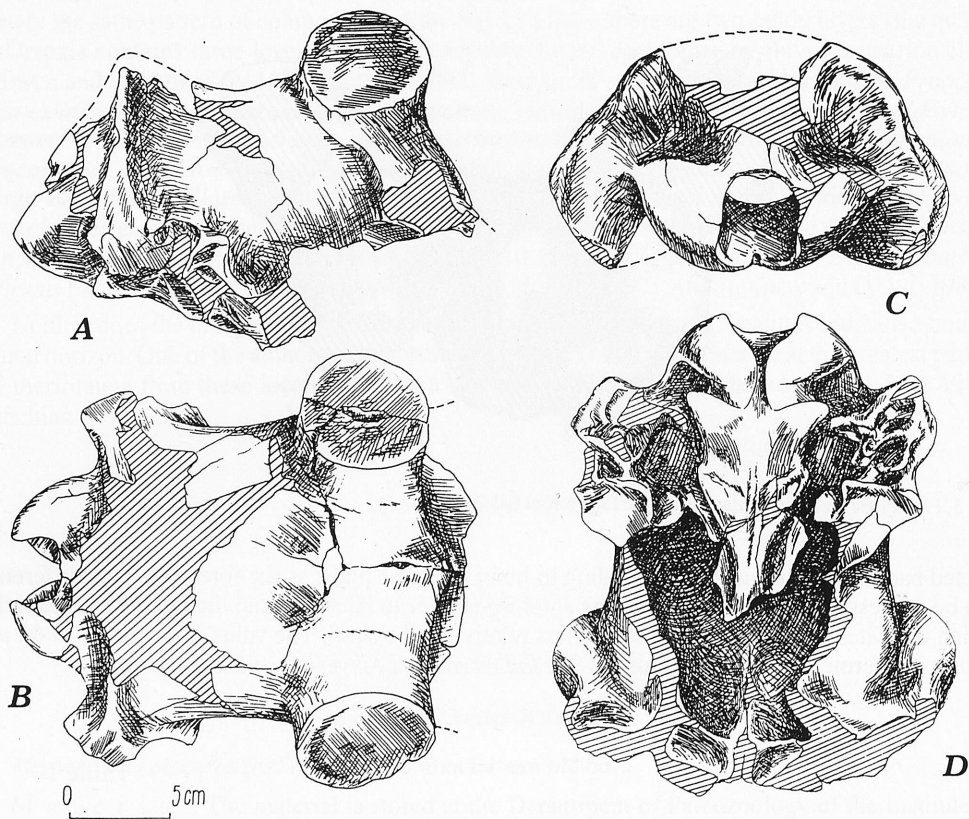
Fig. 4. Skull 53/1 from Firladeni; A – lateral view; B – dorsal view; C – occipital view; D – ventral view.

Early Galerian), while in the skull of *M. verticornis* from Tiraspol (No 1/146; see also KAHLKE 1971), the space between the ventral parts of the condyles is significantly wider. However, this specimen belongs to an old individual and shows a derived morphology with a very short neurocranium.

The measurements of skulls from the Moldovan localities in comparison with those of *M. verticornis* from Tiraspol are given in Table II.

Antlers: The majority of antlers of *M. obscurus* at our disposal are considerably fragmented and the surface of the samples is affected by erosion. A better preserved specimen is the shed right antler from Ursoaia (total length= 320 mm), which shows a very close affinity with the antlers of *M. obscurus* from other European sites. This antler (Fig. 5) has the spurious tine inserted anteriorly and close to the burr (in some samples from Salcia the base of the spurious tine is fused with the burr), and the outer tine in a dorsal position. The basal tines are connected by a ridge that can be observed on the anterior surface of the beam: this character occurs in the antlers of *M. obscurus, M. verticornis*, and in "*M. arambourgi*", as well. The outer tine is well developed; at first it is directed forwards and then bends downwards and outwards; at the base it has a round shape and becomes flattened distally. The beam is almost straight and directed backwards and laterally, its cross-section is elliptical in the basal part, with the major axis subhorizontal, then, above the outer tine, the major axis sets vertically. In this part of the beam the anterior surface is flattened, while the posterior one has a circular outline. The distal portion of this antler seems to be flattened to a greater extent judging by the isolated fragment (Fig. 5).

Table II

Measurements of skull in *M. obscurus* from Moldova and *M. verticornis* from Tiraspol

| Measurements (mm)	*M. obscurus*		*M. verticornis*	
	53/1	52/430	1/146	1/183
Mastoidal breadth	135.0	–	178.5	–
Breadth of frontal contraction	142.3	156.6	184.0	103.0
Breadth of skull behind pedicles	120.0	–	131.0	–
Minimal distance between pedicles tops	83.4	76.3	114.5	143.0
Antero-posterior diameter left pedicle	52.8	–	59.4	43.0
Latero-medial diameter left pedicle	55.0	–	80.0	50.0
Antero-posterior diameter right pedicle	54.2	58.8	61.4	–
Latero-medial diameter right pedicle	56.3	60.0	84.1	–
Breadth of occipital condyls	83.1	–	100.4	–
Length of braincase behind pedicles	74.5	–	55.0	61.0
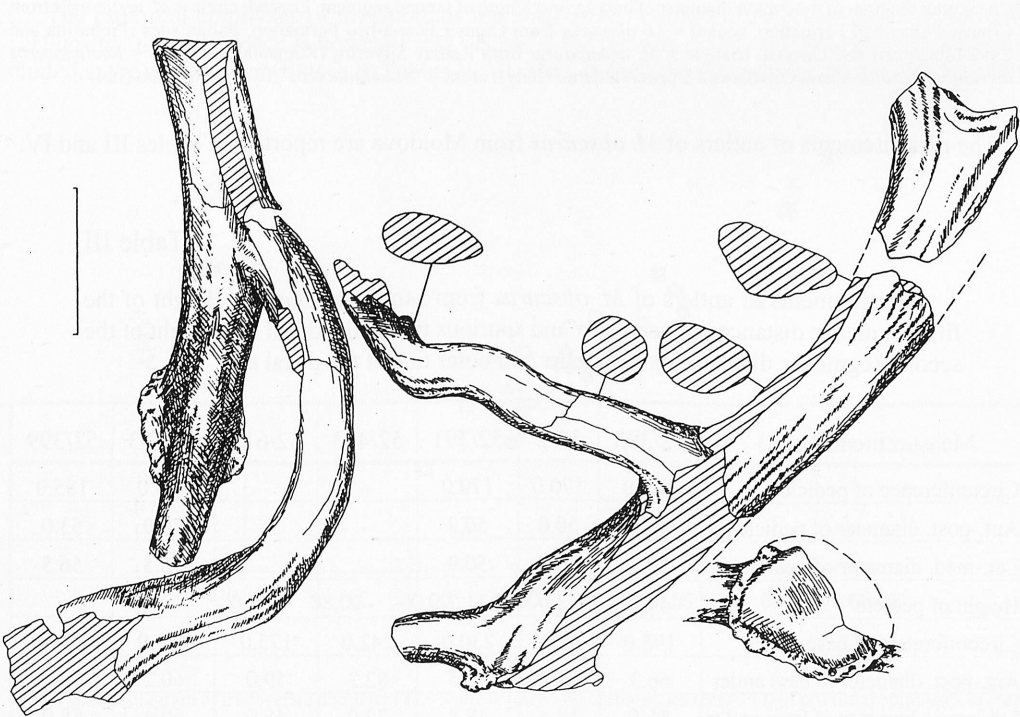
Fig. 5. Shed right antler from Ursoaia. The measure is 10 cm.

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The diagram (Fig. 6) which correlates the maximum diameter of the burr and the length of the second segment (=outer tine-burr distance) evidences that the outer tine tends to be closer to the burr, progressively, from *Eucladoceros* to *M. verticornis*. *M. obscurus,* the juvenile specimens from Petrignano and that of Rotbav-Silvestru are placed in an intermediate position. The shortening of the second segment is probably connected with the reduction of the spurious tine in *M. verticornis.*
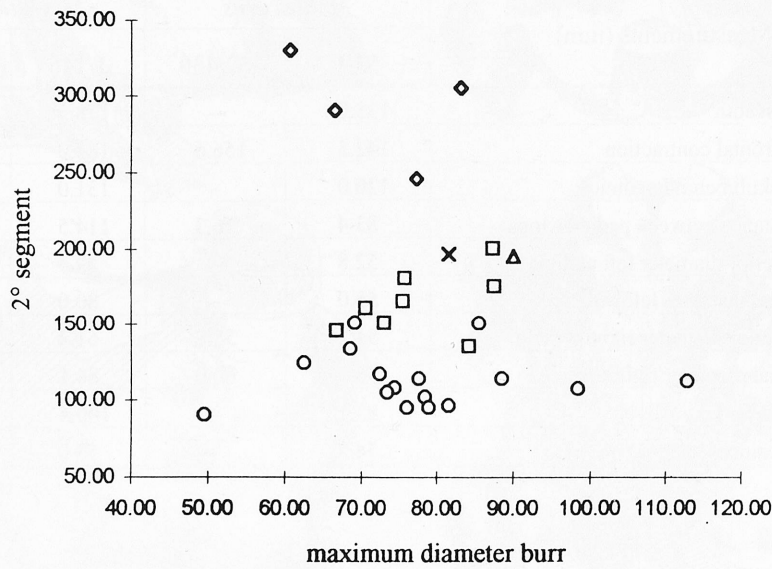

Fig. 6. Scatter diagram of maximum diameter of burr against length of second segment. Legend: circle = *M. verticornis* from Cromer Forest-bed Formation; square = *M. obscurus* from Cromer Forest-bed Formation, Italian sites (Pietrafitta and Cava Liberatori) and Ursoaia; triangle = *M. arambourgi* from Rotbav Silvestru (Romania); rhombus = *Eucladoceros dicranios-ctenoides* from Olivola and Upper Valdarno (Italy); cross = "?*Eucladoceros*" from Petrignano (Italy).

The measurements of antlers of *M. obscurus* from Moldova are reported in Tables III and IV.

Table III

Measurements of antlers of *M. obscurus* from Moldova. Legend: Height of the first segment= distance between burr and spurious tine at the distal endHeight of the second segment= distance between burr and outer tine at the distal end

Measurements (mm)	52/393	15/2	52/391	52/453	52/612	52/403	52/399
Circumference of pedicle	163.0	170.0	170.0	–	–	174.0	185.0
Ant.-post. diameter of pedicle	50.1	50.0	50.9	–	–	50.0	53.0
Lat.-med. diameter of pedicle	50.7	53.2	50.9	–	–	56.5	56.5
Height of pedicle	44.2	52.0	31.7	–	–	–	–
Circumference of base antler	195.0	205.0	230.0	242.0	175.0	183.0	–
Ant.-post. diameter of base antler	66.3	69.5	82.5	82.2	59.0	60.2	–
Lat.-med. diameter of base antler	51.5	59.5	48.8	70.0	45.0	50.4	58.0
Height of 1° segment	48.0	39.0	38.0	56.7	37.0	–	48.2

Table IV

Measurements of antler of *M. obscurus* from Ursoaia. * estimated value

Measurements (mm)		Measurements (mm)	
Ant.-post. diameter burr	87.3	Minimum diameter outer tine	36.8
Circumference burr	258*	Circumference outer tine	147.0
Maximum diameter spurious tine	33.0	Distance base 1°tine-burr	6.6
Minimum diameter spurious tine	36.6	Height of 1° segment	52.6
Circumference spurious tine	115.0	Distance base 2°tine-burr	150.5
Maximum diameter outer tine	47.9	Height of 2° segment	200.0

Legend: Height of 2° segment = distance between burr and outer tine at the distal end.

Dentition: The Salcia quarry yields some isolated teeth of large-sized deer. Since the attribution of these teeth to *Eucladoceros* or *Megaceroides* is practically impossible, they are not dealt with in this paper.

Postcranials: The fossil material from Salcia includes numerous limb bones, mostly fragmented. The specific determination of the postcranial material is difficult because of the presence of both *M. verticornis* and *Eucladoceros* at this site. However, since the majority of antler belongs to *M. obscurus* and the other two species are represented by very few fragmentary remains, we suggest that the majority of postcranial bones belong to the first species. We attempt to point at some characters that allow us to distinguish *M. obscurus* from *M. verticornis*.

The proximal epiphyses of metapodials are smaller in *M. obscurus* from Moldova than in *M. verticornis*; this difference is however less visible if the remains of *M. obscurus* from Italy are included in the comparison (Figs 7, 8; Tables V, VI, VII). In fact, the size of proximal epiphyses of the
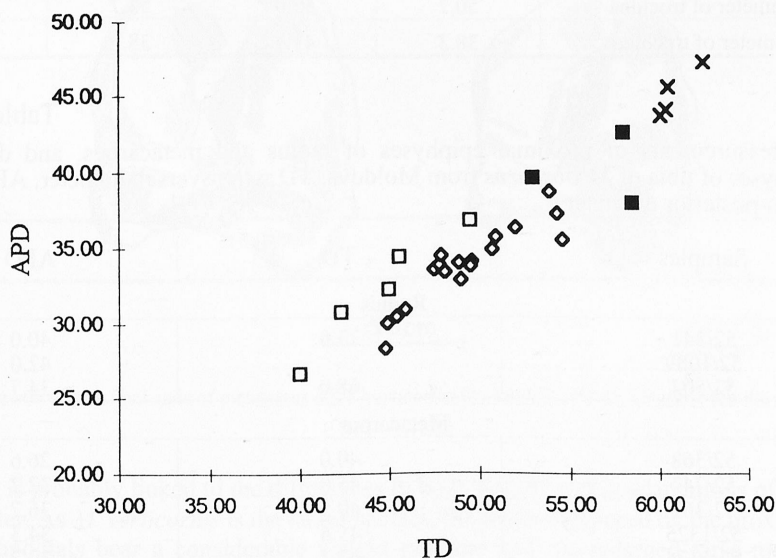

Fig. 7. Scatter diagram of transversal diameter (TD) against antero-posterior diameter (APD) of proximal epiphyses of metacarpus. Legend: cross = *M. verticornis* from various sites; full square = *M. obscurus* from Italian sites Pietrafitta and Cava Liberatori, empty square = *M. obscurus* from Moldova; rhombus = *Eucladoceros dicranios-ctenoides* from Olivola and Upper Valdarno (Italy).
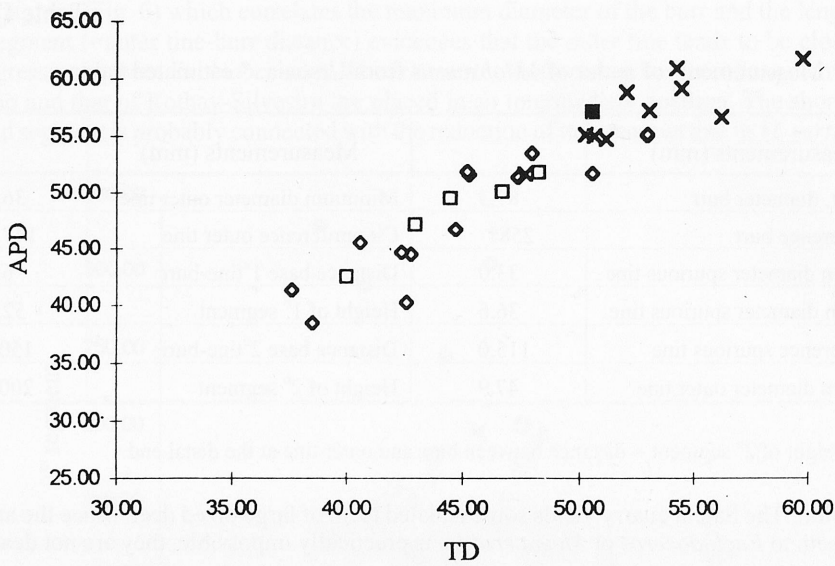
Fig. 8. Scatter diagram of transversal diameter against antero-posterior diameter of proximal epiphyses of metatarsus. Legend: cross = *M. verticornis* from various sites; full square = *M. obscurus* from Italian sites (Pietrafitta), empty square = *M. obscurus* from Moldova; rhombus = *Eucladoceros dicranios-ctenoides* from Olivola and Upper Valdarno (Italy).

Table V

Measurements of distal humerus of *M. obscurus* from Moldova

Measurements (mm)	52/503	52/358	52/1396	52/1328
Breadth of trochlea	69.0	74.3	–	–
Maximal diameter of trochlea	50.2	55.0	53.7	51.7
Minimal diameter of trochlea	38.3	41.1	38.6	39.3

Table VI

Measurements of proximal epiphyses of radius and metacarpus, and distal epiphyses of tibia of *M. obscurus* from Moldova. TD = transversal diameter, APD = antero-posterior diameter

Samples	TD	APD
Radius		
52/341	73.0	40.0
52/1089	–	42.0
52/504	68.0	34.7
Metacarpus		
52/368	40.0	26.6
52/742	45.0	32.2
52/362	49.5	36.7
52/1325	45.6	34.3
52/1326	42.3	30.7
Tibia		
52/267	59.0	44.5
52/264	59.6	46.0
52/359	61.5	49.2

Table VII

Measurements of proximal epiphyses of metatarsus of *M. obscurus* in comparison with *M. verticornis*. Symbols TD and APD as in Table V

Samples	TD	APD
M. obscurus (Salcia)		
52/138	48.3	51.7
52/273	43.0	47.0
52/379	46.7	50.0
52/1339	44.5	49.4
52/268	40.0	42.4
M. verticornis (Tiraspol)		
1/79	54.5	59.0
1/93	54.3	60.8
1/491 (Juvenile)	47.7	51.6

remains from Moldova falls within the range of the Italian *Eucladoceros,* even though the former group shows, on average, a larger antero-posterior diameter than does the latter. The proximal ends of the metatarsals show other differences between *M. obscurus* and *M. verticornis*: the space between anterior and posterior articulations for the naviculocuboideum is short and wide in the former species, while it is long and narrow in the latter (Fig. 9). The difference in size of the proximal end of
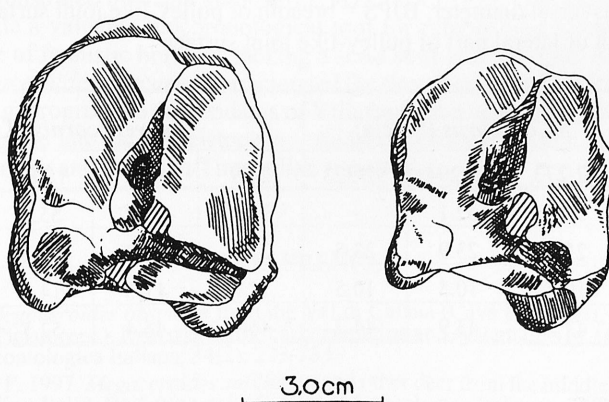

3,0cm

Fig. 9. Comparison of proximal ends of metatarsus of *M. verticornis* (on the left) and *M. obscurus* (on the right).

metatarsals is probably linked to the differences in body weight and in adaptations of the locomotion character. As *M. verticornis* is the larger species, the joints composed by the proximal epiphyses of metapodials bear a considerable weight pressure and the enlarged tarso-metatarsal and carpo-metacarpal joints may be regarded as an adaptation to the increased body weight. Also the distal epiphyses of metatarsals are wider in *M. verticornis* than in *M. obscurus*. This character could be associated with the distal pulley-like joint surface, whose lateral part is wider in the former species, (Fig. 10, see index BLP/BJPS in Table VIII).
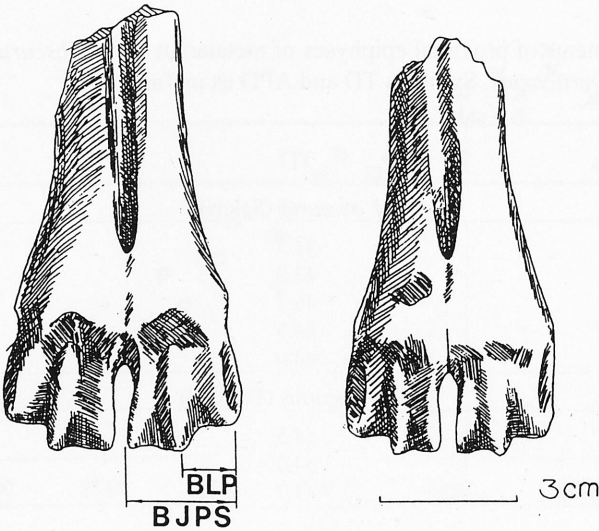
Fig. 10. Comparison of distal ends of metatarsus of *M. verticornis* (on the left) and *M. obscurus* (on the right). BJPS = breadth of the medial pulley-like joint, BLP = breadth of the lateral part of the medial pulley-like joint.

Table VIII

Measurements of distal epiphyses of metatarsus of *M. obscurus* and *M. verticornis*. TD = transversal diameter, BJPS = breadth of pulley-like joint surface (medial), BLP = breadth of lateral part of pulley-like joint surface

Measurements (mm)	*M. obscurus* (Salcia)			*M. verticornis* (Tiraspol)				
	52/273	52/294	52/323	2/79	1/38	1/180	1/153	1/489
TD	52.3	52.1	–	35.0	52.7	55.3	56.1	54.5
BJPS	25.0	23.9	23.5	25.7	25.0	28.2	24.6	27.0
BLP	10.8	10.5	10.5	12.0	11.6	14.8	12.0	12.6
BLP/BJPS	43.2	43.9	44.7	46.7	46.4	52.5	48.8	46.7

In the scatter diagram in Fig. 11 the transversal diameter and the antero-posterior diameter of the distal part of the tibia are compared. Also in this case *M. obscurus* shows lower values than *M. verticornis*.

In observing the scatter diagrams described above, it is worth while to note that the remains of *M. obscurus* from the Italian localities are larger than the Moldovan remains. Differences in size of the same taxon between its populations are frequently observed, the size being controlled by complex interactions between the habitat on one side, and the phenotypic response on the other. However, since the size and robustness increase from *Eucladoceros* to *M. verticornis*, it is justified to suggest that the differences in the dimensions between the Moldavan and Italian populations of *M. obscurus*, are related to the older age of the former.
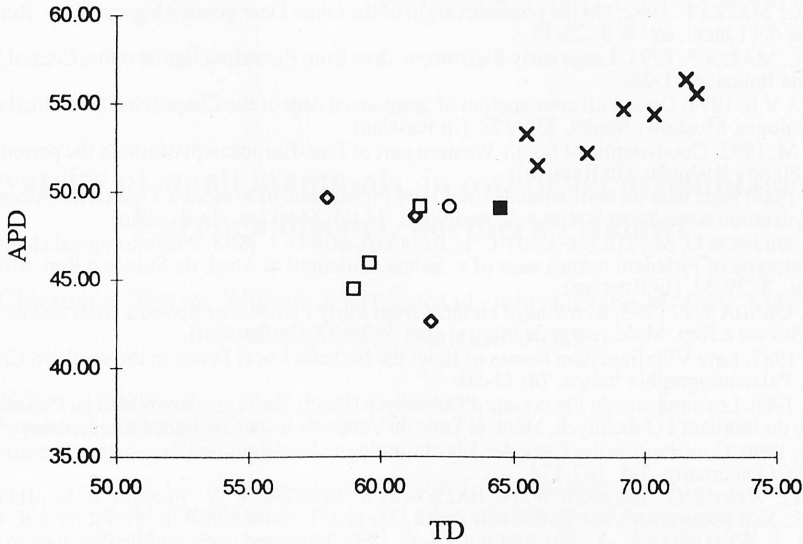
Fig. 11. Scatter diagram of transversal diameter against antero-posterior diameter of distal epiphyses of tibia. Legend: cross = *M. verticornis* from various sites; full square = *M. obscurus* from Italian sites (Selvella), empty square = *M. obscurus* from Moldova; circle = *M. "arambourgi"* from Rotbav Silvestru; rhombus = *Eucladoceros dicranios-ctenoides* from Olivola and Upper Valdarno (Italy).

V. CONCLUSIONS

As already demonstrated by many authors (*i.e.* AZZAROLI 1953; GERAADS 1990, LISTER 1993) deer species provide a valuable biochronological tool for establishing a correlation on a relative chronological scale of faunistic horizons lacking a solid stratigraphic base. As a matter of fact, the occurrence of *Megaceroides obscurus* characterised the timespan during which migrations and evolutionary events (e.g. progressive descendants of Villafranchian taxa) took place, heralding the faunal turnover during the late early Pleistocene – middle Pleistocene, time interval that marks the Villafranchian/Galerian and Odessan/Tiraspolian transition.

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