

Megaceroides obscurus from the Val di Chiana (Cava Liberatori, Tuscany, Central Italy, Farneta f. u., early Pleistocene). Remarks on the early evolution and systematics of *Megaceroides*

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ABSTRACT – *Megaceroides boldrinii* Azzaroli and Mazza, 1992 is considered to be a junior synonym of *Cervus obscurus* Azzaroli, 1953 from the Cromer Forest-bed Formation of Norfolk. This paper describes some remains of this species from Pleistocene sediments in Val di Chiana.

M. obscurus is one of the most primitive representatives of the genus *Megaceroides* known to date. The occurrence of this species in assemblages characteristic of the Farneta f. u. is an important bioevent in the latest Villafranchian.

This species is phyletically linked to *Eucladoceros*.

RIASSUNTO – [*Megaceroides obscurus* della Val di Chiana (Cava Liberatori, Toscana, Italia Centrale, f.u. Farneta, Pleistocene inferiore). Osservazioni su evoluzione e sistematica di *Megaceroides*] – Viene riconosciuta la sinonimia tra *Megaceroides boldrinii* Azzaroli & Mazza, 1992 e *Cervus obscurus* Azzaroli, 1953 rinvenuto nella Cromer Forest-bed Formation. In questo lavoro viene riportata la presenza di *Megaceroides obscurus* in sedimenti del Pleistocene inferiore della Val di Chiana.

M. obscurus è uno dei più primitivi rappresentanti del genere *Megaceroides*. La comparsa di questa specie in associazioni caratteristiche dell'unità faunistica Farneta è un importante bioevento della parte terminale del Villafranchiano.

Questa specie è fileticamente imparentata con *Eucladoceros*.

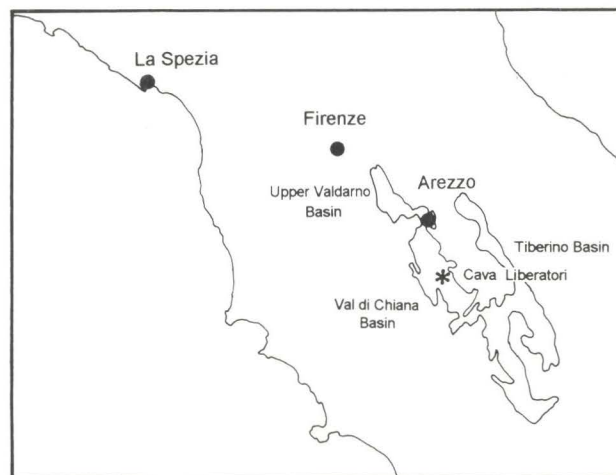
INTRODUCTION

The Val di Chiana (Text-fig. 1), the depression connecting the present valleys of the Arno and Tiber rivers, follows the NNW-SSE trend typical of the Plio-Pleistocene intermontane basins of Central Italy. It is separated from lake Trasimeno by a series of hills which extend for about 30 km. The upper part of the stratigraphic succession that forms the hills consists of a thick unit (about 100 m) of mainly fluvial sands and silts (De Giuli, 1987; Azzaroli, 1993; Masini *et al.*, in press). This sandy unit was extensively quarried in the 60's and 70's, and produced many mammal remains which have been attributed to two distinct faunal assemblages (Azzaroli, 1977a). The earlier assemblage is characterized by the presence of *Mammuthus* (*Archidiskodon*) *meridionalis vestinus*, and is the type fauna of the Farneta faunal unit, which defines the most recent part of the Late Villafranchian. The other assemblage includes remains of *Megaceroides verticornis* (Borgo Nuovo site, Azzaroli, 1976), *Equus caballus* and *Elephas antiquus* (= *namadicus*), (Azzaroli, 1984; De Giuli, 1987), which are characteristic of a Galerian assemblage.

The large sized deer from Cava Liberatori (Text-fig. 1) was found in association with an articulated skeleton of *M. (A.) meridionalis vestinus* (Azzaroli,

1977b), and remains of *Pseudodama farnetensis*, *Lepobos* aff. *vallisarni*, *Equus* aff. *stelhini*, *Equus stenonis*, and a small sized *Stephanorhinus* sp.. The occurrence of *M. (A.) meridionalis vestinus*, *P. farnetensis* and *L.* aff. *vallisarni* dates the assemblage to the Farneta faunal unit.

The deer from Cava Liberatori is referred to *Megaceroides obscurus*, a species defined by Azzaroli (1953) on the basis of antler remains found in the



Text-fig. 1 - Location of Cava Liberatori.

Cromer Forest-bed Formation (East Anglia) and originally named «*Cervus*» *obscurus*. The Author underlined the doubtful systematic position of this large sized deer, even if he recognized an affinity with the genus *Eucladoceros*. In more recent works «*Cervus*» *obscurus* has been referred to the genus *Megaceroides* (Azzaroli, 1979, 1994; Geraads, 1986), but the validity of *obscurus* as a distinct species has been rejected. Several authors (Azzaroli 1979, 1994; Geraads, 1986; Lister, 1993), have considered this form as conspecific with *M. verticornis*, but the consistent occurrence of a large basal tine, and the different orientation of the beams relative to the skull (e.g. slightly diverging antlers) recognizable in *M. obscurus*, are sufficient to consider this species as distinct from *M. verticornis*. It must be underlined that some of the specimens included by Azzaroli (1953) in the species *obscurus*, such as BM 6315 and BM 6307, may possibly be attributed to juvenile specimen of *M. verticornis*.

The specimen BM 2321 from Norfolk (Text-fig. 2), one of the three syntypes reported in the original description of the species is chosen here as the lectotype of *M. obscurus*.

The analysis of the remains referred to *Megaceroides obscurus* stored in the Natural History Museum of London has indicated that this species is conspecific with *Megaceroides boldrinii* Azzaroli & Mazza (1992), from the latest Villafranchian locality of Pietrafitta (Masini *et al.*, 1994; Masini *et al.*, in press). The name *boldrinii* is thus a junior synonym of *obscurus*. In the lignite of Pietrafitta *M. obscurus* is represented by a nearly complete individual, by abundant remains of antlers, some dentitions and postcranial bones (Azzaroli & Mazza, 1993). This

sample thus represents an important point of reference which enriches the knowledge of *M. obscurus*, formerly restricted to fragmentary antlers.

In the localities of East Anglia where the remains of *M. obscurus* have been found (Mundesley, Trimmingham and Overstrand), sediments referred to the Pre-Pastonian, Pastonian and Cromerian stages occur (cf. Lister, 1993). *M. obscurus* represents a primitive species of *Megaceroides*, distinct from the middle Pleistocene megalocerines, like *M. verticornis*. One can thus form the hypothesis that the remains of *M. obscurus* from the Cromer Forest-bed Formation, lacking a precise reference of the provenience, come from sediments referable to early Pleistocene, younger than those that yielded *Eucladoceros ctenoides*, *Cervalces gallicus*, (Gibbard *et al.*, 1991; Lister, 1993). This conclusion is in agreement with the biochronological position of the same species from the latest Villafranchian assemblages of Pietrafitta and Cava Liberatori. However the occurrence of taxa from the latest Villafranchian of the Cromer Forest-bed Formation has already been reported. Remains of *Eucladoceros tetraceros*, a species well represented at Peyrolles in the French Central Massif (dated between 1.2-1.06 Ma, cf. Bonifay, 1990), have been in fact recovered at Overstrand and East Runton (Azzaroli, 1953; Lister, 1993).

SYSTEMATICS

MEGACEROIDES OBSCURUS (Azzaroli, 1953)

«*Cervus*» *obscurus* Azzaroli, 1953 (Figs. 42-45, pp. 74 - 75)

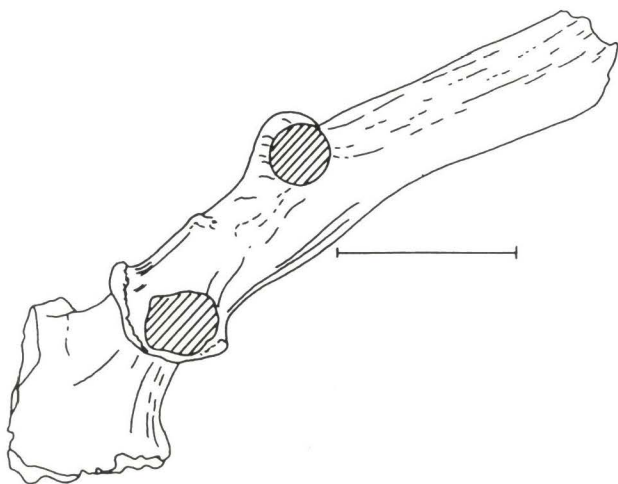
Synonymies:

- 1956 *Orthogonoceros verticornis* - KAHLKE, p. 30.
- 1979 *Megaceros verticornis* pro parte - AZZAROLI, p. 11.
- 1986 *Praemegaceros verticornis* - GERAADS, p. 145.
- 1992 *Megaceroides boldrinii* AZZAROLI & MAZZA, pp. 29-31, figs. 4, 5.
- 1993 *Megaceroides verticornis* - AZZAROLI & MAZZA, p. 9, fig. 9.
- 1994 *Megaceroides verticornis* pro parte - AZZAROLI, p. 128.

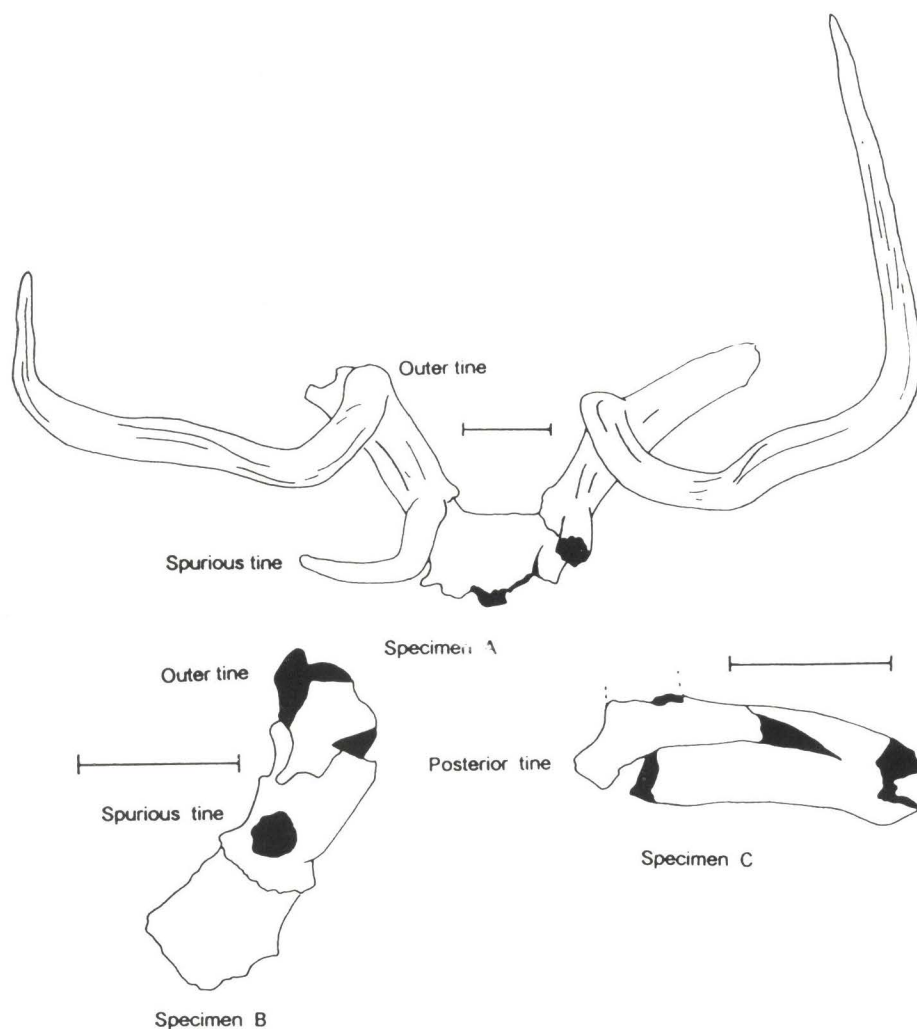
Megaceroides obscurus from Cava Liberatori (Pl. 1, figs. 1-3)

Material - Specimen A: incomplete antlered skull and fragments of the premaxilla, maxilla, and nasal bones; specimen B: proximal fragment of the beam inserted in the pedicle; specimen C: intermediate part of beam; P2/ and a second phalange.

Description - The terminology proposed by Azzaroli & Mazza (1992a; 1993) is used to describe the antlers (Text-fig. 3).



Text-fig. 2 - Lectotype of *Megaceroides obscurus* (BM2321, NHM of London). The scale is approximately 10 cm.



Text-fig. 3 - Terminology of tines in specimens from Cava Liberatori is shown. The scale is 10 cm.

The antler structure of the megalocerine from Cava Liberatori is like that of *Megaceroides obscurus* from the Cromer Forest-bed Formation and Pietrafitta. There are two closely spaced tines on the proximal section of the beam; a lower tine inserted anteriorly (spurious tine), and a second well developed, dorsally positioned tine (outer tine). The latter displays a characteristic shape, initially bending down, then outwards, and finally upwards (Pl. 1, figs. 1, 2), and is extremely well developed. The beam between the spurious and outer tines is semicircular in section, with a flattened anterior surface and a ridge on the upper side which joins the two basal tines. The intermediate segment of the antler bears no tines. At the point where a barely noticeable, posteriorly positioned tine is located (Text-fig. 3, specimen C), the beam turns sharply upward, forming a right angle, so that its upper part is nearly vertical. The morphology of the distal part of the antler is unknown.

The antlers diverge at an angle of about 90° , and are directed backwards (Pl. 1, fig. 2). Faint bony ridges border the bases of the pedicles. The forehead is longitudinally slightly convex.

The measurements of the beams and tines are given in Table 1.

The morphology of the forehead, the presence of the spurious tine, and the cylindrical shape of the outer tine are characteristic of the genus *Megaceroides*. The development of the spurious tine and the slight degree of divergence of the beams are characteristic of *M. obscurus*.

The second upper premolar (occlusal length = 18.2 mm; basal length = 18.3 mm; maximum width = 18.4 mm) has a deep lingual groove.

The second phalange displays no systematically significant characteristics. The dimensions of these finds are, however, in agreement with their attribution to a megalocerine form.

Measurements	Ar	Al	B	nn	1014	1016	1017	1018
Maximum pedicle diameter	*57.0	55.0	59.9	45.6	--	--	--	--
Maximum burr diameter	*77.0	75.7	72.6	*70.5	84.0	73.0	66.7	79.2
Minimum burr diameter	*70.0	*65.0	68.6	*61.0	*80.0	--	53.2	69.5
Maximum diameter beam above burr	79.7	--	79.9	70.0	*83.0	--	--	--
Minimum diameter beam above burr	*56.4	--	49.8	*58.0	--	--	--	--
Maximum diameter beam above 1st tine	61.3	52.7	*69.0	51.3	72.0	--	60.0	--
Minimum diameter beam above 1st tine	52.7	51.5	56.7	38.0	--	--	45.0	--
Maximum diameter beam above 2nd tine	--	60.2	--	42.7	80.2	--	--	--
Minimum diameter beam above 2nd tine	--	49.4	--	37.6	--	--	--	--
Burr-1st tine (basal) distance	13.4	9.1	11.5	21.5	12.0	--	--	--
Burr-1st tine (distal) distance	46.5	39.6	61.7	57.9	53.0	52.0	54.0	54.0
Burr-2nd tine (basal) distance	150.0	112.0	99.5	118.9	94.2	97.0	--	--
Burr-2nd tine (distal) distance	212.0	180.0	--	160.0	135.0	145.0	--	--
Basal distance 1st-2nd tine	152.0	112.7	89.7	--	--	--	--	--
Distal distance 1st-2nd tine	165.0	125.0	87.9	101.4	89.0	105.0	104.0	--
Maximum thickness 1st tine	43.7	--	*54.0	41.7	40.0	--	48.0	40.8
Minimum thickness 1st tine	37.3	--	32.9	32.0	30.0	--	30.0	32.2
Maximum thickness 2nd tine	54.0	50.7	*65.0	42.6	38.8	*40.0	--	--
Minimum thickness 2nd tine	45.0	45.0	45.4	34.1	--	--	--	--
Straight length 1st tine	270.0	--	--	180.0	--	--	--	171.0

Tab 1 - Measurements (mm) of antlers in *Megaceroides obscurus* from Cava Liberatori (specimens A and B) and Pietrafitta (from nn to 1018). * Estimated measurements.

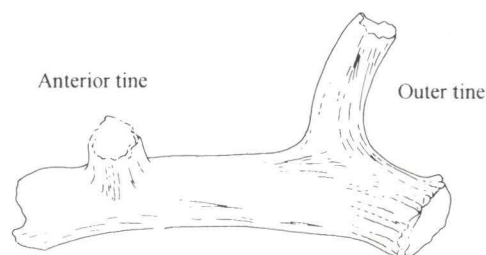
DISCUSSION

M. obscurus is one of the most primitive representatives of the genus *Megaceroides* found in Europe, and is therefore important in defining the bioevents which occurred in the later part of the Villafranchian.

Megaceroides is characterized by divergent antlers in their lower half, which in the more derived forms tend to lie almost horizontal. The distal segment of the beam is vertical. A first tine (= spurious tine) which generally is reduced to a knob in the derived species as *M. verticornis*, may occur close to the burr, though it is completely lacking in many specimens of this species.

The horizontal segment of the beam bears a second dorsal tine (= outer tine), and, generally, an intermediate tine (= anterior tine) (Text-fig. 4). There is a posteriorly located tine where the beam bends sharply upwards.

In one of the most recent reconstructions of the earliest phases of the evolution of the genus *Megaceroides*, Azzaroli and Mazza (1992a, 1993) argue that *Megaceroides* and *Eucladoceros* are closely linked. According to these authors, the beginning of the change of the antler structure (e.g. direction and curvature of the beam, number, position and shape



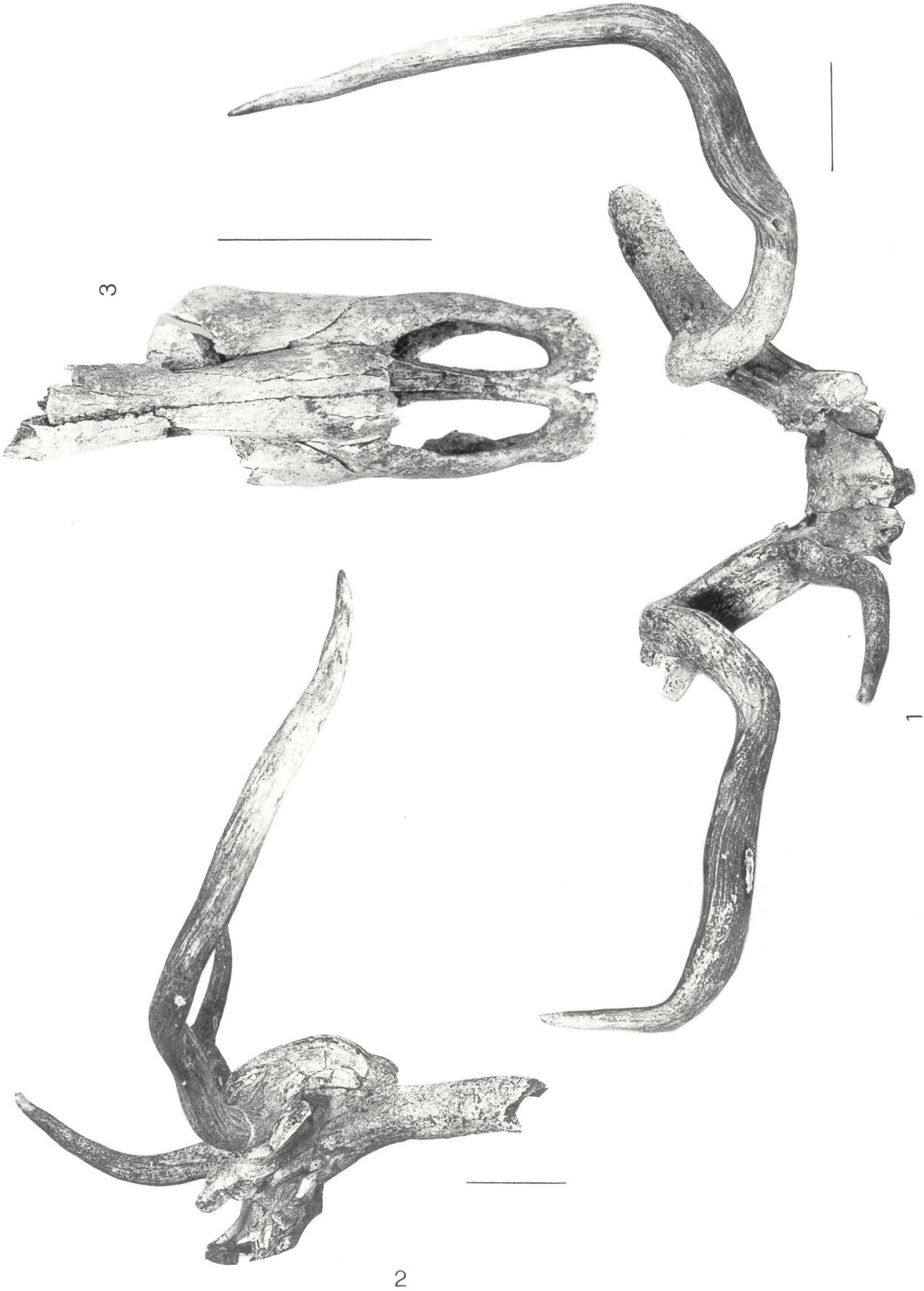
Text-fig. 4 - Outer tine and anterior tine in *Megaceroides verticornis* from Süssenborn (from Kahlke, 1956, redrawn). 1/4 of the natural size.

of the tines) leading to the morphology of *Megaceroides*, may be recognized in *Eucladoceros boulei* from the late Pliocene or early Pleistocene locality of Nihowan, China (Teilhard de Chardin & Piveteau, 1930). The population of *Eucladoceros boulei* found in Nihowan is characterized by a considerable individual variability, and indeed some of the specimens display morphologies similar to those of megalocerines, with strongly diverging beams, and tines that Azzaroli and Mazza consider to be homologous with those of *Megaceroides*. Following this hypothesis the first true megalocerine «stage» is represented by *Megaceroides* (= *Psekupsoceros*) *orientalis* (Radulesco & Samson, 1967) from Psekups,

EXPLANATION OF PLATE 1

Figs. 1-3 - *Megaceroides obscurus* from Cava Liberatori. The scale is 10 cm.

- 1) Specimen A. Frontal view.
- 2) Specimen A. Lateral view.
- 3) Specimen A. Premaxilla, maxilla and nasal bones.



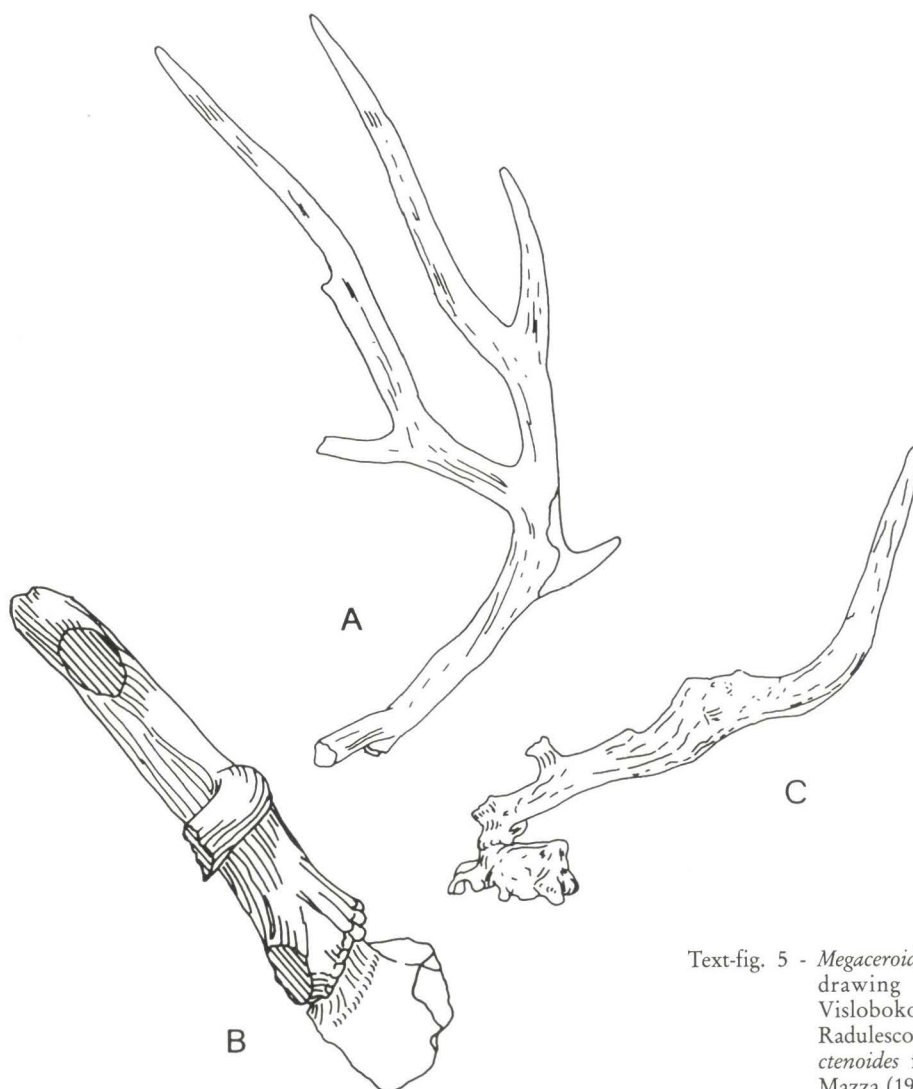
Caucasus (correlated with the subchron Olduvai and to the end of the Middle Villafranchian, cf. Pevzner & Vangengeim, 1986). The systematic position of this species is however uncertain, because it is based on a single specimen, an antler whose reconstruction may not be entirely reliable. Specifically, the supposed presence of a posterior tine at the point where the beam bends, becoming vertical, may be wrong (Text-fig. 5a, Vislobokova, pers. comm.). If, in place of this tine, which is characteristic of the megalocerines, the beam is extended backwards, as suggested by Vislobokova (pers. comm.), the specimen would be similar to *Eucladoceros*, which is the interpretation of several authors (Vislobokova, 1990; cf. Radulesco & Samson, 1967).

Vislobokova and Changkang (1990) suggested that the *Megaceroides* (= *Praemegaceros*) lineage might derive from *Orchonoceros gromovi*, a species from

the late Pliocene of Mongolia and Trans-Baikalia. According to the descriptions the skull and the antler morphology of *O. gromovi* are similar to those of *Megaceroides*, though its antlers do not yet display the characteristic bending of the beam that generally occurs at the posterior tine. According to Vislobokova and Changkang the earliest specimens attributable to *Megaceroides*, (*M. sp.*, Vislobokova, 1990) have been found in early Galerian assemblages of Tadzhikistan (Lakhuti) and Trans-Baikalia (Zasuhino).

Unfortunately the cited works lack in sufficient figures which might allow a deep and more critical approach.

Several fossils with morphologies intermediate between those of *Eucladoceros* and *Megaceroides* have significantly contributed to the understanding of the early evolution of megalocerines in Europe. Among

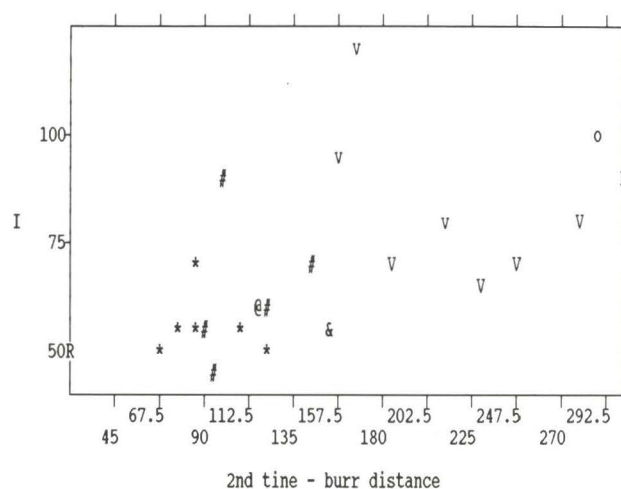


Text-fig. 5 - *Megaceroides* (= *Eucladoceros*) *orientalis* (A) from drawing and photo provided by Dr. I. Vislobokova; *Megaceroides arambourgi* (B) from Radulesco & Samson (1967), redrawn; *Eucladoceros ctenoides* from Petignano (C) from Azzaroli & Mazza (1992b), redrawn.

these, the specimen (R.S.1) referred to *Allocaenelaphus arambourgi* (Text-fig. 5b), from the Rumanian locality of Rotbav-Silvestru (Late Villafranchian, Radulesco & Samson, 1967), displays features which warrant its attribution to the genus *Megaceroides* and place it very close to *M. obscurus*. For example, the second tine is dorsally positioned and tends to bend downwards, and the postcranials are larger and stronger than those observed in *Eucladoceros*. On the other hand, the presence of a well developed first basal tine, and, most of all, the dorsal position of the intermediate tine evidence an affinity with *Eucladoceros*. The mixture of megalocerine and eucladocerine characters suggests that the species is transitional between the two genera, and supports the hypothesis of their possible relationship.

Despite some megalocerine characters as the general structure of the antlers, the presence of an outer downward curved tine located dorsally on the beam, the size and robustness of its postcranial elements, *M. obscurus* itself presents some analogies with *Eucladoceros* (Azzaroli & Mazza, 1993). Indeed, the skull has large ethmoidal vacuities and deep preorbital pits and the mandible is not pachyostotic. Besides, the beams of the antlers do not diverge widely, and have well developed first tines.

Intermediate characters between those of *Eucladoceros* and *Megaceroides* can be also observed in a skull fragment with connected antlers, stored at the Paleontological Museum of the University of Florence (Text-fig. 5c). This specimen (IGF 13742), that has been attributed to a juvenile *Eucladoceros ctenoides* (cf. Azzaroli & Mazza, 1992b), was found in a sand quarry near Petrignano, in the Val di Chiana. The presence of a second dorsal tine that tends to turn downward, and a possible posterior tine, where the beam appears to bend upwards, are reminiscent of megalocerine morphology. A comparison of the measurements taken on the proximal part of antlers referred to *Eucladoceros* and *Megaceroides* supports the close similarity to *Megaceroides* of the specimen from Petrignano. Indeed, when the ratio between the maximum diameter of the second tine and the maximum diameter of the burr (= I, which expresses the strength of the outer tine), is plotted against the proximal distance between the outer tine and the burr, the data fall in two distinct groups (Text-fig. 6). The former group, including the megalocerine forms attributed to *M. obscurus* and *M. verticornis*, is characterized by antlers with low I values and short distances between the outer tine and the burr; the second, including remains attributed to *E. dicranios* and *ctenoides* from Olivola and the Upper Valdarno



Text-fig. 6 - Scatter diagram of proximal distance of the outer tine from the burr against I (= greater diameter of outer tine/greater diameter of burr) * 100.

Legend:

= *Megaceroides obscurus* from Pietrafitta and Cava Liberatori.

@ = *Megaceroides obscurus* from unspecified site in Val di Chiana.

* = *Megaceroides verticornis* from various Italian localities (Colle Curti, Borgo Nuovo, Cortiglione Monferrato, unspecified sites in Val di Chiana).

& = *Eucladoceros ctenoides*, Petrignano.

v = *Eucladoceros dicranios*, Upper Valdarno.

V = *Eucladoceros ctenoides*, Upper Valdarno.

o = *Eucladoceros dicranios*, Olivola (f.u.).

(Tasso f.u.), corresponds to higher values for both ratio and length. The specimen from Petrignano plots close to the megalocerines group.

COMPARISONS

Despite the characteristics shared with the genus *Eucladoceros*, *M. obscurus* displays a number of morphological features which allow its referral to *Megaceroides*. In particular, the resemblance of its antlers to those of *M. verticornis*, evidences the close affinity between the two species. The presence of a large spurious tine tends however to distinguish the former form from *M. verticornis* found in the localities of Forest bed. These remains display a fair degree of morphological stability with regard to the proximal part of the antler, where the spurious tine is rarely larger than a small knob, and may even be absent. The same kind of variability in the morphology of this tine is shown by *M. verticornis* from other early and middle Galerian localities (e.g. Süssenborn, Kahlke, 1956-59, 1969; Voigtstetd, Kahlke, 1958, 1965; Borgo Nuovo, Azzaroli, 1976; Colle Curti, Ficarelli & Silvestrini, 1991). In the course of time the spurious tine tends to disappear in

the genus *Megaceroides*, as is demonstrated by its absence in middle Galerian populations, such as in the *M. solilhacus* from Isernia (Abbazzi and Masini, in progr.).

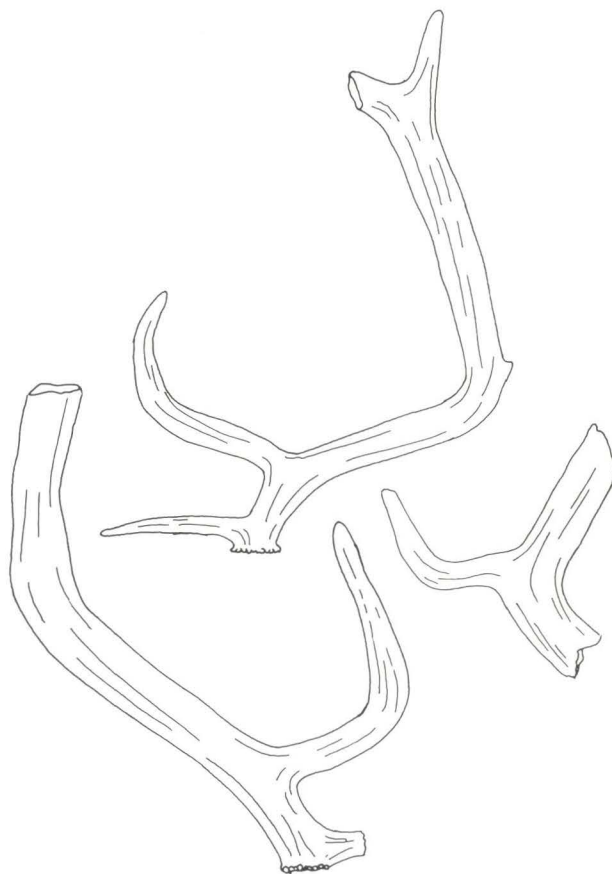
The orientation and the antero-dorsal location of the outer tine observed in *M. obscurus* are diagnostic characters shared with *M. verticornis*; on the other hand the former character is not observed in *M. solilhacus*, where the outer tine is also reduced. The exceedingly great development of this tine in the specimen A from Cava Liberatori does not have any particular taxonomic significance, because of the variability and frequent anomalies displayed by deer antlers. The fact that the lengths of the left and right tines of this individual differ macroscopically confirms the unsuitability of this detail for systematic considerations.

The absence of the anterior tine is of doubtful diagnostic value. In fact, specimens of *M. verticornis* without this character have been found in some Italian localities as Colle Curti and Borgo Nuovo, and in *M. obscurus* from Pietrafitta, while this same feature is common in the *M. verticornis* populations of Süssenborn (Kahlke, 1956-59; 1969), Voigtstedt (Kahlke, 1958; 1965), Mosbach (Kahlke, 1960) and Forest Bed (Azzaroli, 1953, and personal observations).

On the other hand the posterior tine is always present in the genus *Megaceroides*. The poor development of this tine observed in specimen C is attributable to ontogenetic factors. In fact the analysis of the material from the Pietrafitta population has shown that this tine reached various phases of development, depending upon the age of the individual and the stage of the yearly development of the antler. Indeed, the posterior tine appears to have been completely absent even in adults, if the antler had not yet completed its annual growth (Text-fig. 7).

Finally, the slight degree of divergence of the beams (about 90°), in *M. obscurus* from East Anglia, Pietrafitta and Cava Liberatori further distinguishes this species from *M. verticornis*.

In the dentition, Azzaroli and Mazza (1992a, 1993) consider the lingual groove observed in the P2/ from Pietrafitta and Cava Liberatori as a further evidence of the link between *Eucladoceros* and *Megaceroides*. Indeed this feature seems to appear consistently in the P2/ of *Eucladoceros dicraniosctenoides* from Olivola and the Upper Valdarno. The lingual groove could thus prove useful to distinguish *M. obscurus* from the more recent species of *Megaceroides*, in the absence of more significant remains, such as antlers connected to the skull or beam fragments in which the proximal section is preserved. However, one cannot but wonder if both

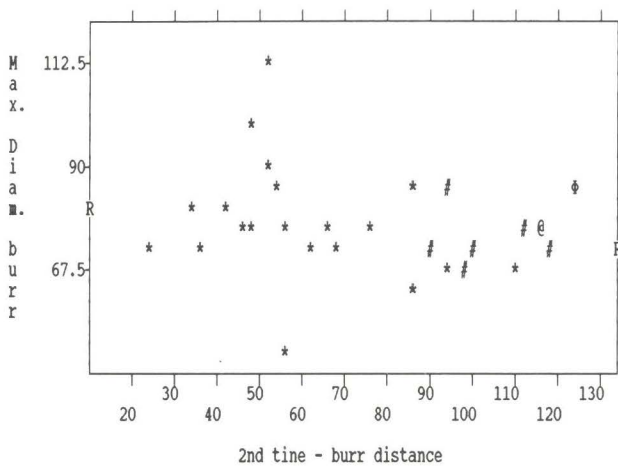


Text-fig. 7 - Different phases of the development of posterior tine in *Megaceroides obscurus* from Pietrafitta.

morphotypes might be present in *M. obscurus* populations, since the samples are not sufficiently large, and examples of megalocerines of the *verticornis* group that display this character have been mentioned in the literature (e.g. Voigtstet; cf. Kahlke, 1958).

Bony ridges surrounding the inner sides of the pedicles are present in the skulls from Cava Liberatori (specimen A), Pietrafitta and in the lectotype from Norfolk. These ridges have been observed in many *Megaceroides* specimens, and therefore do not appear to have a diagnostic meaning within the genus.

Finally, the comparison of the measurements taken on the antlers of *M. obscurus* and *M. verticornis* did not turn out to be useful for distinguishing the two species, though the outer tine tends to be more distant from the burr in *M. obscurus*. Indeed, the poor development, or the absence of the spurious tine in *M. verticornis* may be responsible for the tendency of the outer tine to be located closer to the burr (Text-fig. 8). The greater dispersion observable in the *M. verticornis* population might in part be due



Text-fig. 8 - Scatter diagram of proximal distance of outer tine from the burr against maximum diameter of the burr.

Legend:

* = *Megaceroides verticornis* (Borgo Nuovo, Colle Curti, Cortiglione Monferrato, Cromer Forest-Bed, (°) Mosbach).

= *Megaceroides obscurus* (Pietrafitta, Cava Liberatori).

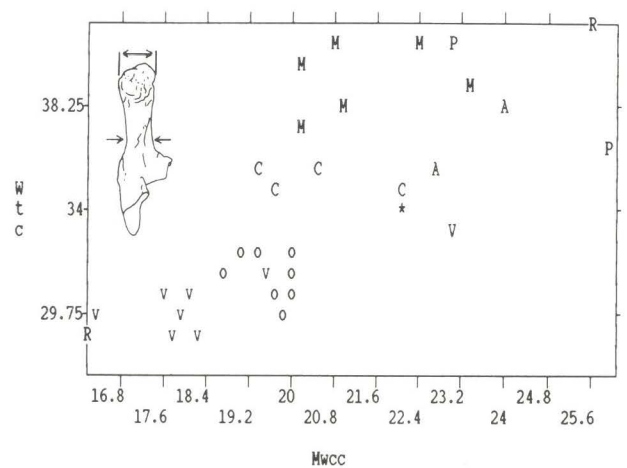
Φ = *Megaceroides obscurus* (Norfolk, Cromer Forest-Bed Formation).

@ = *Megaceroides obscurus* (Val di Chiana, unsp. site).

(°) = Data from literature (Kahlke, 1960)

to the inclusion of young individuals, which tended to display a greater distances between the outer tine and the burr.

The revision of large sized deer remains from other sites in Val di Chiana has allowed the recognition of *M. obscurus* outside of Cava Liberatori. The locality of Selvella has yielded postcranial remains of a large sized deer previously attributed to *Eucladoceros* cf. *dicranios* (De Giuli, 1987; Azzaroli & Mazza, 1992b). The large size, the robustness, and the morphology of the remains, combined with their biochronological position (they are associated with elements referable to the Farneta faunal unit, including *Pseudodama farnetensis*, Azzaroli, 1992, and a derived form of *Equus stenonis*, De Giuli, 1987) has already led to the suggestion of their conspecificity with *M. obscurus* (Abbazzi, 1991). The recognition of this species at Cava Liberatori, from sedimentary levels correlatable with those of Selvella, increases the plausibility of its occurrence at Selvella. In Text-fig. 9 and 10 the dimensions of metacarpal and calcaneum of eucladocerines from Olivola and Upper Valdarno (*E. dicranios* and *E. ctenoides* from several sites referred to the Tasso faunal unit), and of megalocerines from early and middle Galerian



Text-fig. 9 - Scatter diagram of minimum width of corpus calcanei (Mwcc) against maximum width of tuberosity (Wtc).

Legend:

P = *Megaceroides obscurus* from Pietrafitta.

* = *Megaceroides obscurus* from Selvella.

C = *Megaceroides verticornis* from Colle Curti.

M = *Megaceroides solihacus* from Venta Micena (°).

A = *Megaceroides* sp. from Cava Pirro (Apricena, Foggia).

V = *Megaceroides* sp. from Upper Valdarno.

v = *Eucladoceros dicranios-ctenoides*, from Upper Valdarno

o = *Eucladoceros dicranios*, Olivola (f.u.)

(°) Data from literature (Menendez, 1987).

localities are plotted. One may note that the dimensions of the *M. cf. obscurus* specimens from Selvella (indicated with *) fall within the range of variability of *Megaceroides*.

In the Capellini Museum of Bologna, several remains of antlers from unspecified localities within the Val di Chiana are preserved. In particular, one of these may be referred to *M. obscurus* on the basis of the development of its spurious tine (Text-fig. 11) and of the more posterior orientation of the beam relative to the skull.

CONCLUSIONS

The systematic, stratigraphical, and biochronological studies recently carried out on the mammal assemblages from Late Villafranchian localities (Torre *et al.*, 1992; Masini *et al.*, in press) have produced a fairly detailed picture of the events that characterized the upper part of this Mammal Age in the Italian Peninsula. In the Late Villafranchian mammal assemblages, one can observe the first occurrences of totally new taxa (e.g. primitive bison-tine at Cava Pirro, Masini *et al.*, in press) which

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