

Megaceroides solilhacus and other deer from the middle Pleistocene site of Isernia La Pineta (Molise, Italy)

Laura ABBAZZI

Dipartimento di Scienze della Terra
Università di Firenze

Federico MASINI

Dipartimento di Geologia e Geodesia
Università di Palermo

KEY WORDS – Cervidae, Systematics, Middle Pleistocene, Middle Galerian, Isernia La Pineta, South Italy.

ABSTRACT – Deer remains recovered at the middle Pleistocene (middle Galerian) site of Isernia La Pineta, are revised. A well diversified assemblage made up of *Megaceroides solilhacus*, *Cervus elaphus* cf. *C. e. acoronatus*, *Dama* cf. *D. clactoniana* and *Capreolus* sp. has been identified. The systematics of *M. solilhacus* and its relationships with the other species of the genus *Megaceroides* are discussed. The overall structure of the antlers of *M. solilhacus* suggests that this species is closely related to *M. verticornis*. Nevertheless the absence of the spurious (first) tine, the tendency to a strong reduction of the outer (second) tine, and the widely divergent beams, in the antlers of *M. solilhacus*, can be considered derived features within the genus *Megaceroides*.

RIASSUNTO – [*Megaceroides solilhacus* e gli altri cervidi del sito del Pleistocene medio Isernia La Pineta (Molise, Italia)] – Vengono analizzati i resti di cervidi recuperati nella località del Pleistocene medio (Galeriano medio) Isernia La Pineta. Lo studio ha evidenziato un'associazione ben diversificata composta da *Megaceroides solilhacus*, *Cervus elaphus* cf. *C. e. acoronatus*, *Dama* cf. *D. clactoniana* e *Capreolus* sp.. Vengono discussi la sistematica di *M. solilhacus* ed i suoi rapporti con le altre specie del genere *Megaceroides*. L'assetto generale dei palchi di *M. solilhacus* suggerisce l'esistenza di uno stretto legame con la specie *M. verticornis*. Tuttavia l'assenza del primo pugnale, la marcata tendenza alla riduzione del secondo e l'ampia divergenza delle aste nei palchi di *M. solilhacus* possono essere considerate caratteristiche derivate all'interno del genere *Megaceroides*.

INTRODUCTION

Isernia La Pineta (Text-fig. 1), an important Lower Paleolithic settlement of Central Italy, has yielded a large amount of faunal remains, the refuse of prehistoric hunters (Coltorti *et al.*, 1981; Cremaschi *et al.*, 1985). The anthropic horizons, which consist of several surfaces of occupation that are considered to be geologically coeval, overlie a thick lacustrine sequence capped by a travertine rich formation, and are in turn overlain by four meters of fluvial sediments containing two distinct paleosols (Cremaschi, 1983). K/Ar radiometric determinations carried out on the biotites of the tuffaceous horizons, one of which overlies the fossiliferous deposit (ITA18), and the other of which correlates with the anthropic horizons (ITA20), have yielded ages of 0.68 ± 0.066 My and 0.73 ± 0.07 My, respectively (Sevink *et al.*, 1981). A repetition of the determinations on the sanidines contained in the sediments overlying the second of the anthropic surfaces yielded an age of 0.736 ± 0.04 My (Coltorti *et al.*, 1981, 1982; Delitala *et al.*, 1983). The results of a paleomagnetical analysis carried on by McPherron & Schmidt (1983) have led the students to refer the human inhabitation surface to the late reversed Matuyama magnetochrone, basing also on the radiometric ages (see also Coltorti *et al.*,

1982). In fact, as reported by the same authors, the results of this study must be considered as preliminary and a further sampling of the sedimentary succession would be necessary.

A recent analysis of the freshwater mollusk



Text-fig. 1 - Location map of Isernia La Pineta locality.

fauna found in the fluvio-lacustrine sediments underlying the anthropic horizons (Kotsakis *et al.*, 1992) has revealed taxa indicative of a cold, humid climatic phase tentatively referred by the authors to the ^{18}O isotopic stage 22.

Large mammals are represented by broken bones, mostly medium to large sized, which prehistoric man used, after butchering the animals, along with broken tools, discarded chips from their stone working, and blocks of travertine which were used to consolidate the marshy ground near a stream (Cremaschi *et al.*, 1985). The fluvial sediments overlying the anthropic levels have yielded remains of small vertebrate (Sala, 1983). Some of the elements in the assemblage have been revised since the preliminary species list was published (Sala, 1983). The macromammals include *Elephas namadicus* (= *antiquus*), *Stephanorhinus hundsheimensis* (Sala & Fortelius, 1993), *Hippopotamus antiquus* (Mazza, 1996), *Sus scrofa*, *Bison schoetensacki* (Sala, 1987), *Megaceroides solilhacus* (this paper), *Cervus elaphus* cf. *acoronatus* (this paper), *Dama* cf. *D. clactoniana* (this paper), *Capreolus* sp. (discussed here), *Hemitragus bonali*, *Ursus* cf. *deningeri*, *Panthera leo fossilis* (Sala, 1990), and *Lepus* cf. *europaeus*. The micromammals include *Talpa* gr. *europaea*, *Pliomys episcopalis*, *Pliomys lenki*, *Clethrionomys* sp., *Arvicola cantiana*, *Microtus* (*Terricola*) sp., *Microtus breccensis*, and *Microtus* gr. *arvalis-agrestis*. Arvicolidids predominate.

The faunal assemblage has been referred to the middle Galerian (Sala *et al.*, 1992; Gliozzi *et al.*, 1995), a biochronological unit that also includes the assemblages from Valdemino (Tozzi, 1969), Visogliano (Cattani *et al.*, 1991; Gliozzi *et al.*, 1995), Maur, Mosbach (Brüning, 1978; Koenigswald & Tobien, 1987), Hundsheim (Toula, 1902), and L'Escaie (Bonifay, 1981; Chaline, 1972).

In this paper, the deer remains excavated between 1979 and 1992, as well as a few antlers found *in situ* on the paleosurface exposed in November 1990, are revised.

SYSTEMATICS

INTRODUCTION

Though deer remains make up only a small fraction of the large mammals found at the site, they reveal a diversified assemblage. The following taxa were identified:

Megaceroides solilhacus
Cervus elaphus cf. *acoronatus*
Dama cf. *D. clactoniana*
Capreolus sp.

The largest species, *M. solilhacus*, is well represented, while remains of the smaller sized species are scarce. This suggests that humans preferentially selected large skeletal remains, a fact that can also be observed in the other taxa that make up the assemblage. In the case of *M. solilhacus*, the elements privileged were the antlers, which are most numerous.

Family CERVIDAE Gray, 1821

Subfamily CERVINAE Baird, 1857

Tribe MEGALOCERINI Viret, 1961

Genus MEGACEROIDES Jouleaud, 1914

MEGACEROIDES SOLILHACUS (Robert, 1829)

Pl. 1, figs. 1-5

Material

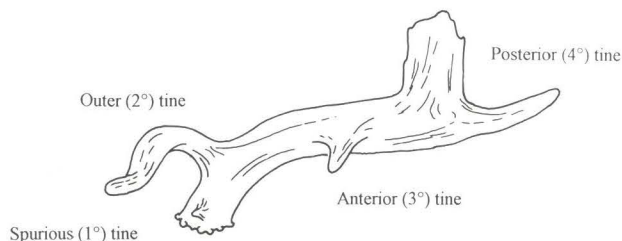
Antlers: IS21957 - shed left antler; IS21843 - left antler with part of forehead; IS22026 - shed right antler; IS29293 - right antler; IS33057 - right antler with part of forehead; IS89/836 - shed right antler; IS81 - shed left antler (juvenile); IS2611 - shed left antler; IS2579 - shed right antler; IS (1) - shed right antler; IS (2) - shed right antler; IS (3) - right antler with part of forehead; IS (4) - shed antler.

Dentitions: IS33088 - right mandible with M3-M2; IS30132 - left M/1 or M/2; IS2550 - left M/3; IS2553 - right P/2; IS2557 - right D3/; IS2558 - fragment of M/3; IS30132 - left M/2.

Post-cranial skeletal elements: IS31/B36 - left cubonavicular; IS2607 - left cubonavicular; IS30270 - right calcaneus; IS2600 - II phalange; IS15 - III phalange; IS2605 - distal portion of right metacarpus; IS2606 - distal portion of right metacarpus; IS2610 - right capitotrapezoide; IS2611 - right scaphoid.

Description

Antlers and foreheads (Pl. 1, figs. 1-4) - The terminology of antler elements is according to Azzaroli & Mazza, 1993 (Text-fig.2).



Text-fig. 2 - Terminology of the tines in *Megaceroides* as proposed by Azzaroli & Mazza, 1993.

As a group, the remains display a marked morphological homogeneity. Parts of the foreheads are preserved, as well as the proximal section of the antler up to a few centimeters beyond the base of the posterior tine, a few fragments of the palmation, and a few small isolated tines. Many of the finds were deformed by pressure in dorso-ventral and antero-posterior direction. The measurements of antlers are reported in Tab. 1.

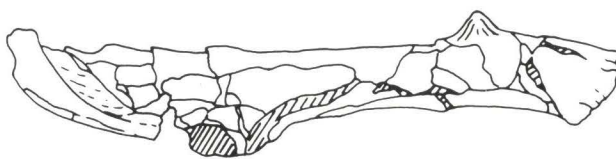
The pedicles are located on the frontal plane, and are strongly divergent. The beams, which are considerably shortened, are directed almost laterally, forming an angle of about 80° with the sagittal plane, as can be observed directly on the specimens in which some part of the frontal is preserved (IS21483 and IS 29293). The plane of the burr is inclined relative to the beam, with which it forms a characteristic angle of about 60°.

The beam presents an initial, slight dorsally convex curvature, then it is almost straight, bending down slightly before the point at which the inferior surface rotates upward and laterally. In dorsal view almost all beams display a curve that is concave caudally, at the height of the anterior tine.

The beams are sub-cylindrical at the base, and gradually become flattened, beginning from the anterior (=third) tine and beyond the attachment of the posterior tine. Even though the distal part of the beam was not preserved in any of the specimens, the discovery of a few isolated fragments suggests that there was a palmation, topped along its margins by small points.

The most proximal section of the beam, which is free from tines, presents an antero-dorsal knob located between 62 and 115 mm from the burr. In three specimens (IS22026, IS89/836, IS NN2) this knob is missing, while it is slightly accentuated in specimen IS 81, which is attributable to a young in-

dividual (Text-fig. 3). The position of the knob and its tendency to bend slightly down in this young individual reveal its homology with the outer (=second) tine of *Megaceroides verticornis*. A tine in a middle-anterior position, homologous with the anterior tine of *M. verticornis*, is invariably present, and is strongly flattened at the base. In the specimens in which it is best preserved, it initially curves upwards (e.g. IS21843). Finally, there is a posterior tine, located at the point where the beam twists upwards.



Text-fig. 3 - IS 81, shed right antler of juvenile specimen. The antler is strongly crushed. The scale bar is 10 cm long.

Dentition - Because of the scantiness of finds, no specific conclusions about the dental morphology can be drawn. The teeth are fairly brachyodont, and their dimensions (Tab. 2) fall within the range of variation for the genus *Megaceroides*. The third lower molars have labial columns (ectostylids) between the first, second, and third lobes, and have a pronounced cingulum on the mesio-labial side. The presence of interlobal columns and the development of a cingulum on the tooth wall are relatively variable characters in deer populations, and are therefore of little systematic importance, at least in the absence of a sufficiently numerous sample population. The mandible fragment is pachyostotic (Pl. 1, fig. 5).

Post-cranial skeleton (Tabs. 3-6) - A mor-

Sample	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
IS21957	101.5	82.3	115.2	144.0	220.0	81.0	62.0	0.0	0.0	70.0	47.0	0.0	0.0	0.0	0.0	60
IS21843	86.0	82.0	96.3	166.0	263.0	76.0	74.0	64.0	59.0	69.0	54.0	0.0	0.0	0.0	0.0	60
IS220026	74.1	72.6	77.3	161.0	239.0	67.0	64.0	60.0	52.0	56.0	54.0	360.0	366.0	189	100.0	65
IS33086	102.0	85.0	62.6	0.0	0.0	81.0	75.0	76.0	67.0	68.0	66.0	0.0	0.0	0.0	0.0	70
IS89/836	77.0	74.7	0.0	135.0	268.0	71.0	63.0	68.5	51.5	66.0	53.0	0.0	360.0	0.0	0.0	55
ISNN2	95.0	88.0	0.0	210.0	285.0	0.0	0.0	62.5	60.0	0.0	0.0	390.0	0.0	0.0	0.0	55
ISNN3	85.0	0.0	65.0	180.0	0.0	0.0	0.0	68.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	70
IS82	60.1	57.0	95.1	175.0	252.0	45.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	175	252.0	65

Tab. 1 - Antlers of *Megaceroides solilhacus* from Isernia. Measurements in mm.

Legend: 1 - Maximum diameter of burr. 2 - Minimum diameter of burr. 3 - Distance from knob (= outer tine) to burr. 4 - Distance from basal end of third tine to burr. 5 - Distance from distal end of third tine to burr. 6 - Maximum diameter of beam above burr. 7 - Minimum diameter of beam above burr. 8 - Maximum diameter of beam at the knob. 9 - Minimum diameter of beam at the knob. 10 - Maximum diameter of beam above knob. 11 - Minimum diameter of beam above knob. 12 - Distance from burr to upwards curvature of beam. 13 - Distance from burr to upward curvature, measured anteriorly. 14 - Distance from knob to basal end of third tine (=anterior tine). 15 - Distance from knob to distal end of third tine. 16 - Angle formed between the plane of the burr and the axis of the beam.

Sample	OL	NL	W	H
M/3 IS2550	33.6	37.3	16.7	18.0
M/3 IS2552	0.0	0.0	17.6	18.0
M/2 IS30132	27.2	25.7	18.1	10.0
P/2 IS2553	15.7	16.4	10.7	14.4
D /3 IS2557	22.7	20.5	17.8	9.3

Tab. 2 - Teeth of *Megaceroides solilhacus* from Isernia. Measurements in mm.

Legend: OL - Occlusal length. NL - Neck length. W - Maximum width. H - Height of the crown.

phometric study that included data on other species of the genus *Megaceroides* from some European Late Villafranchian and Galerian localities has shown that the post cranial elements of the Isernia population fall within the range of variation of this genus. In particular, the dimensions of one of the two distal metacarpal fragments (IS 2606) fall at the higher end of the range (Text-fig. 4).

The bodies of the cubonaviculars are more flattened than those of the other species examined (*Megaceroides* sp. from Cava Pirro, *M. obscurus* from Selvella, and *M. verticornis* from Voigtstedt), as is indicated by their higher L1a/3 ratio (Tab. 3). This datum, which is also confirmed by the greater flattening of the trapezoid, suggests that the limbs of the Isernian megalocerine were stouter than in the other species considered.

Critical remarks on the genus *Megaceroides*

Azzaroli and Mazza (1993) have recently raised the name *Megaceroides* to generic rank; it unites the

Sample	1a	1b	1c	2a	2c	3	1a/3
IS2607	51.5	0.0	0.0	46.1	41.6	21.6	2.45
IS31/b36	55.8	55.5	45.1	54.9	40.6	22.4	2.49
PN5	58.2	57.9	48.5	54.6	45.9	26.6	2.18
9P	54.1	53.6	0.0	47.0	43.2	23.8	2.27
31A	58.0	57.3	48.2	51.4	47.1	28.0	2.10
IGF14158	57.0	56.4	45.0	49.9	39.7	27.4	2.08
VOI749	60.6	58.2	45.5	58.5	46.5	26.8	2.26
VOI289	59.1	57.8	46.1	57.1	45.6	27.3	2.16
VOI1750	53.4	50.9	41.9	51.8	40.1	25.7	2.07
VOI96	57.6	57.2	46.6	58.9	43.9	23.7	2.43
VOI370	59.4	56.7	45.4	58.8	45.9	26.0	2.28
VOI545	61.4	60.0	49.8	58.8	45.9	26.0	2.36

Tab. 3 - Comparison of cubonaviculars of *Megaceroides* from some European localities. IS2607 and IS 31/b36 from Isernia; PN5, 3P, 31A *Megaceroides* sp. from Pirro Nord; IGF 14158 *M. obscurus* from Selvella (Val di Chiana); VOI from 749 to 545 *M. verticornis* from Voigtstedt. Measurements in mm.

Legend: 1a - Maximum width. 1b - Proximal articular width. 1c - Articular width of the talar face. 2a - Maximum thickness. 2b - Articular width of the calcaneal face. 3 - Height of the lateral side.

Sample	1	2	3	4	5
IS30270	129.5	102.0	142.2	37.8	24.6

Tab. 4 - Calcaneus of *Megaceroides solilhacus* from Isernia. Measurements in mm.

Legend: 1 - Maximum width of the body of calcaneus. 2 - Dorsal length of the body of the calcaneus. 3 - Width of the calcaneal tuberosity. 4 - Minimum width of the body of the calcaneus.

species previously referred to *Megaloceros* (*Megaceroides*). According to the rules of priority, the type species of the genus is *Megaceroides algericus* (Lydekker), 1890. This species however, does not present all the diagnostic characters common within the group. It presents in fact many apomorphies, being one of the younger species of *Megaceroides*.

Even if the application of the rules of priority is in our opinion questionable for such a case, we agree, for the present work, to the proposal of Azzaroli & Mazza.

The morphology of the antlers, the dorsal location of the outer tine, and the convex profile of the forehead of the Isernia megalocerine are characteristic of the genus *Megaceroides* (Azzaroli, 1952). This genus forms a clade that includes a number of closely related forms, upon whose specific status the researchers have not yet reached agreement (cf. Azzaroli, 1953, 1979, 1994; Geraads, 1986; Hadjouis, 1990; Kahlke, 1956; Radulesco & Samson, 1967;

Sample	1	2	3	4	5	6	7
IS2605	27.3	56.1	35.5	62.5	37.2	30.1	34.6
IS2606	0.0	65.0	36.0	67.5	40.5	31.0	37.2

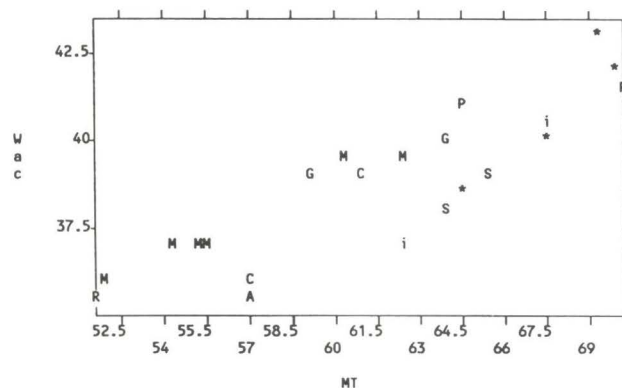
Tab. 5 - Metacarpus of *Megaceroides solilhacus* from Isernia. Measurements in mm.

Legend: 1 - Minimum thickness of the diaphysis. 2 - Supra-articular width of the distal epiphysis. 3 - Supra-articular thickness of the epiphysis. 4 - Maximum articular thickness of the distal epiphysis. 5 - Width of the articular crest of the lateral condyle. 6 - Width of the abaxial hemicondyle of the lateral condyle. 7 - Width of the axial hemicondyle of the lateral condyle.

Sample	1	2	3	4	5	6	7	8	9
IS2600	54.5	46.6	33.3	29.1	23.5	22.4	22.4	33.4	23.6

Tab. 6 - II Phalange of *Megaceroides solilhacus* from Isernia. Measurements in mm.

Legend: 1 - Maximum length. 2 - Axial length. 3 - Anatomical length. 4 - Thickness of the proximal end. 5 - Width of the proximal end. 6 - Minimum thickness of the diaphysis. 7 - Minimum width of the diaphysis. 8 - Thickness of the distal end. 9 - Width of the distal end.



Text-fig. 4 - Scatter diagram of the width of the articular crest of the lateral condyle (Wac) against maximum thickness of the distal epiphysis (MT) of metacarpus in *Megaceroides*.

Legend: i = *Megaceroides solilhacus*, Isernia. A = *M. sp.*, Cava Pirro (Foggia). C = *M. obscurus*, Selvella (Val di Chiana). P = *M. obscurus*, Pietrafitta (Perugia, Umbria). M = *M. aff. solilhacus*, Venta Micena (data from Menéndez, 1987). S = *M. verticornis*, Süssenborn. * = *M. verticornis*, Voigtstedt. G = *M. aff. verticornis*, Akhalkalaki (data from Vekua, 1986).

Vislobokova, 1990). In our opinion, within Europe, the Middle East, and North Africa, and excluding the many endemic species of the Mediterranean islands, the genus includes the following species.

- *Megaceroides algericus* (Lydekker, 1890), is the type species of the genus. It is the most recent form of *Megaceroides* (late Pleistocene, from Algeria and Morocco; Joleaud, 1916; Arambourg, 1938; Hadjouis, 1990), and, by comparison with the European continental forms, presents many endemic characteristics. It is of smaller size, and is characterized by a number of apomorphies, including thickening of the forehead, a short snout, widely divergent antlers, the shortening of the horizontal section of the beam, with the loss of the spurious tine and a tendency towards the loss of the outer tine. The pedicles are high and thick. The mandible is distinctly pachyostotic, the premolars are reduced, and the P/4 is strongly molarized. These characteristics are associated with marked brachyodonty (Hadjouis, 1990). This species, which displays a melange of derived and primitive features, may be an offshoot of *M. verticornis*, or it represents an independent, closely related, lineage.

- *Megaceroides obscurus* (Azzaroli, 1953), both the most primitive and the earliest species (Farneta F.U. of the Late Villafranchian, early Pleistocene), is known from the presumably late Villafranchian

levels of the Cromer Forest-bed Formation and from late Villafranchian sites of Central Italy (Abbazzi, 1995). It is characterized by not-palmate antlers, which are slightly divergent, and which have a well developed, basally located spurious tine. There is no anterior tine, and the end of the beam has few branches. In the skull, the ethmoidal fissures are broad.

Megaceroides boldrinii, described by Azzaroli & Mazza (1992, 1993) on the basis of specimens found at Pietrafitta (Farneta faunal unit, Late Villafranchian), is a junior synonym of *Megaceroides obscurus* (Abbazzi, 1995). «*Allocaenelaphus*» (= *Megaceroides*) *arambourgi* (Radulesco & Samson, 1967) based on fragmentary remains is still under discussion, and may be another primitive early Pleistocene megalocetine identical, or closely related to *M. obscurus*.

- *Megaceroides verticornis* (Dawkins, 1872) is the best documented species, and was widely distributed, from Western Europe (England, France, Germany, Italy) to the Caucasus and Israel. The beams are characterized, in the proximal section, by a marked dorsal twist, by a reduced or absent spurious tine, and by the outer tine, which is well developed, although usually smaller than in *M. obscurus*, and displays a characteristic initial downwards curvature. The anterior tine varies from flattened to oval in cross section, and is sometimes absent (e.g. samples from Süssenborn, Kahlke 1956-1959; Borgonuovo, Azzaroli, 1976; Cortiglione Monferrato, De Alessandri, 1903; Colle Curti, Ficarelli & Silvestrini, 1991, and Haliakmon, Melentis, 1967). Both antlers with palmate (e.g. the Pakefield skull from England) and ramified vertical sections have been attributed to this species; for the latter Ambrosetti (1967) has proposed the subspecific denomination *M. verticornis dendroceros*.

M. verticornis has been found in many Italian localities, though only the better documented finds from the localities of Ponte Galeria (Ambrosetti, 1967), Borgonuovo, Cortiglione Monferrato, Colle Curti, and Imola (Azzaroli & Mazza, 1993), all of which seem to be limited to non-palmate forms, have been described.

- *Megaceroides solilhacus* (Robert, 1829) is based on a few specimens collected in different sites (Robert, 1829; Moullade, 1886) in the surroundings of Solilhac (Upper Loire, France; Thouveny & Bonifay, 1984). The lectotype was defined and illustrated by Azzaroli in 1979 (Table IV, Fig. 1 a, b). This species is characterized by the absence of the spurious tine, and the tendency to a strong reduc-

tion of the outer tine. The distal part of the horizontal section of the beam is flattened, and the end is broad, palmate, pointed, and has many small points on the posterior edge. The remains from many middle Pleistocene European localities have been referred to this species. In Italy, *M. solilhacus* has been identified at Terranera (Venosa Basin, Basilicata; Montezemolo, 1964; Caloi & Palombo, 1979), at Ponte Milvio (cfr. Caloi & Palombo, 1986), Notarchirico (Venosa Basin; Belli *et al.*, 1991), and recently at the Cesi locality in the Colfiorito Basin (Ficcarelli *et al.*, in progress). Azzaroli (1979) also refers to this species the megalocerine remains from Voigtstedt that Kahlke (1958, 1965) attributed to *M. sp.*, and those from Akhalkalaki (Southern Georgia) attributed to *Megaceroides* aff. *verticornis* by Vekua, (1986). Finally, Menéndez (1987) refers the megalocerine from Venta Micena (early Pleistocene of Spain) to *M. solilhacus*, and this species has been found repeatedly in other Spanish early Pleistocene localities (cf. Moyà-Solà & Menéndez, 1986). The deer from Venta Micena however, probably represents a closely related, but distinct species from *M. solilhacus*, and its systematical position will be discussed below.

- *Megaceroides dawkinsi* (Newton, 1886) is a smaller sized form that is known only from England (Azzaroli, 1953). Like *M. solilhacus*, it presents a tendency towards the simplification and shortening of the horizontal part of the beam, with the loss of the spurious tine and a considerable reduction of the outer tine. The terminal parts of the beams have never been described, though palmate sections from the Cromer Forest-bed Formation are preserved in the Museum of Norfolk (A. Lister, pers. comm.). The strong resemblance between *M. dawkinsi* and *M. solilhacus* suggests that these species could be closely related (Abbazzi *et al.*, work in progr.).

M. dawkinsi has recently been found in the English locality of Little Oakley (Lister *et al.*, 1990), where it is associated with *M. verticornis*. The fossiliferous horizons, which yielded the remains of a highly derived *Miomys savini*, are referable to the lower part of middle Pleistocene (Middle to Late Cromerian, after pollen stratigraphy).

Discussion

The considerable morphological variability of the antlers and the mosaic distribution of the characters among the populations have caused some confusion in the literature for what concerns the distinction between the species *M. verticornis* and *M.*

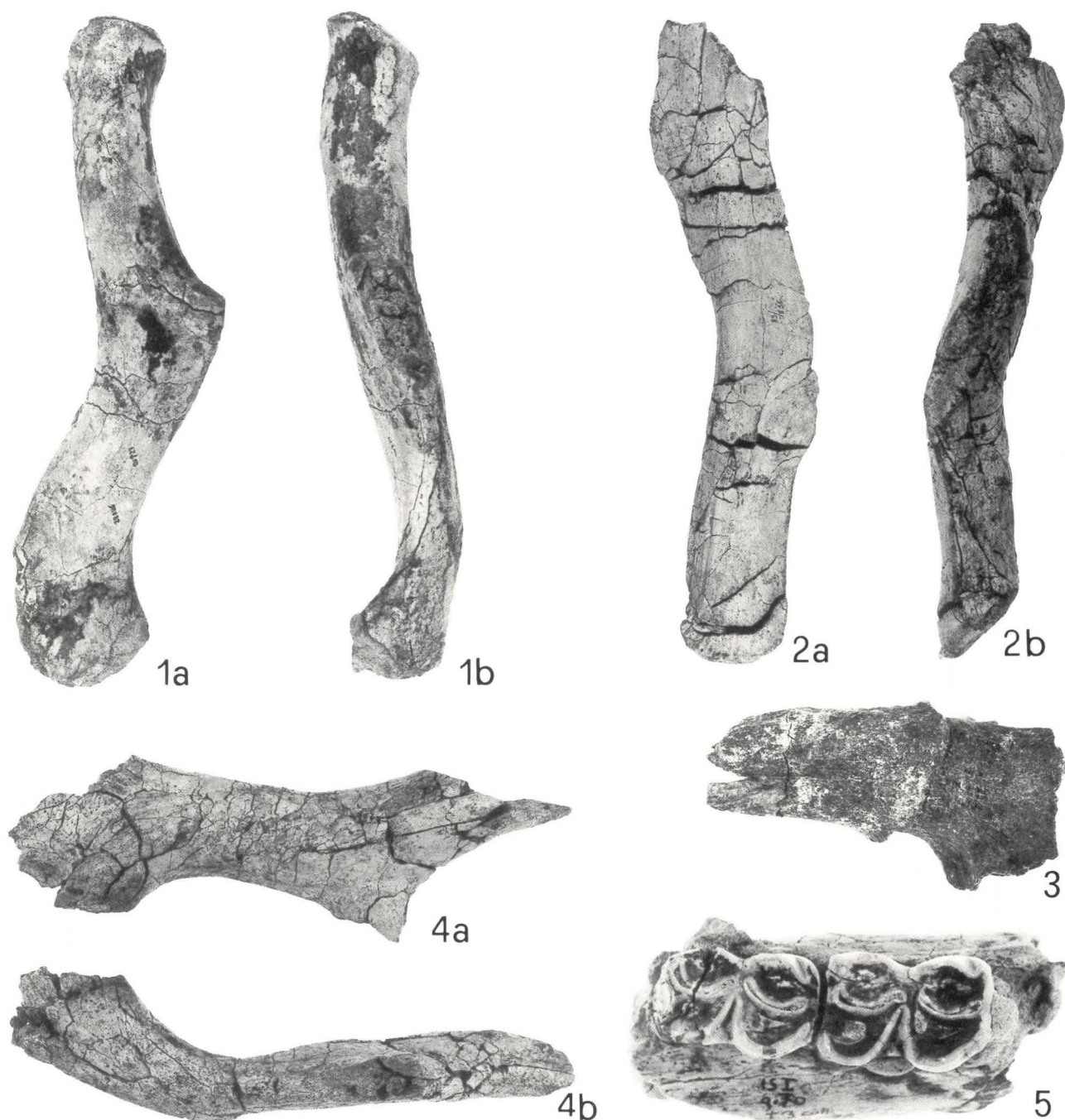
solilhacus. The relatively high number of antlers found at Isernia allowed us to reexamine the problem of the definition of *M. solilhacus*.

The antlers from Isernia display a series of characters that also occur in the specimens from Solilhac and Terranera, and which are distinct from those of *M. verticornis*:

- tendency to lose the curvature of the proximal section of the beam;
- shortening of the horizontal section of the beam;
- absence of the spurious tine;
- marked tendency towards the reduction and loss of the outer tine.

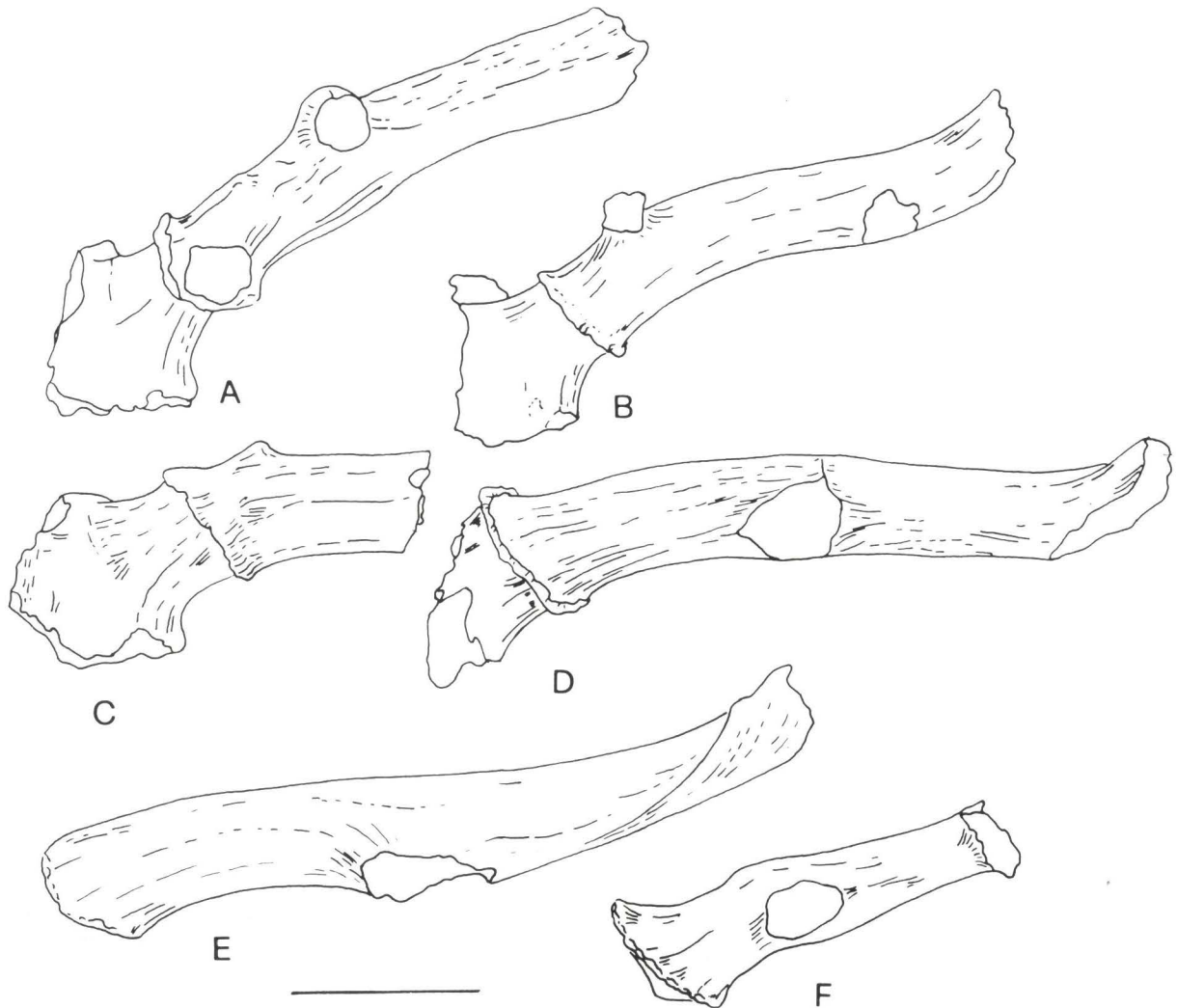
Within the genus these characteristics can be considered derived (Text-fig. 5), and they occur also in *M. algericus*, the endemic species of the late Pleistocene of North Africa, and in *M. dawkinsi*. Besides, even though the cited characters, if taken singly, may reenter within the range of morphotypes displayed by *M. verticornis*, their consistent presence in the sample from Isernia argues in favor of their diagnostic value, and shows that this cervid belongs to the species *M. solilhacus*.

The inclusion of many forms within the species *M. solilhacus* (Azzaroli, 1979), has broadened the definition of the species, and rendered the distinctions between it and *M. verticornis* difficult. Of particular importance in the definition of *M. solilhacus* is the presence, at Voigtstedt, Süssenborn, and Mosbach, of a form originally defined by Kahlke (1956-59, 1958, 1960, 1965, 1969) as *Megaceroides* (= *Orthogonoceros*) sp., which displays some characters intermediate between those of *M. verticornis* and the type material of *M. solilhacus*. *M. sp.* shares with *M. solilhacus* the tendency to be larger in size, a pointed palmation (cf. Voi 358), the fourth lower premolar with a more pronounced labial groove, and the mandible slightly pachyostotic. On the basis of these characteristics Azzaroli (1979) referred the specimens from Voigtstedt, which are better represented, to *M. solilhacus*, an attribution that Geraads (1986) and Menéndez (1987) consider questionable. The *Megaceroides* sp. from Voigtstedt has a well developed outer tine, and the horizontal section of the beam is fairly long, with a marked proximal curvature. These characteristics commonly occur in the antlers of *M. verticornis*, while they do not in those of *M. solilhacus*. The pointed form of palmation is, in our opinion, of little significance, mainly because it occurs in specimens that can be attributed to *M. verticornis* on the basis of other characteristics (e.g. antler Süss 7982 in Kahlke, 1956; pers. observ.). Even if the variability of the distal section of the beam is on the whole



EXPLANATION OF PLATE 1

- Figs. 1-5 - *Megaceroides solilhacus* from Isernia.
 1) IS 22026, shed right antler: a) dorsal view, b) frontal view; 2) IS 89/836, shed left antler: a) dorsal view, b) frontal view.
 3) IS 33087, right antler with part of forehead, frontal view. 4) IS 29293, right antler: a) dorsal view, b) frontal view.
 5) IS 33080 right mandible with fragment of M3 and M2, natural size. All the antlers are about 1/4 of the natural size.



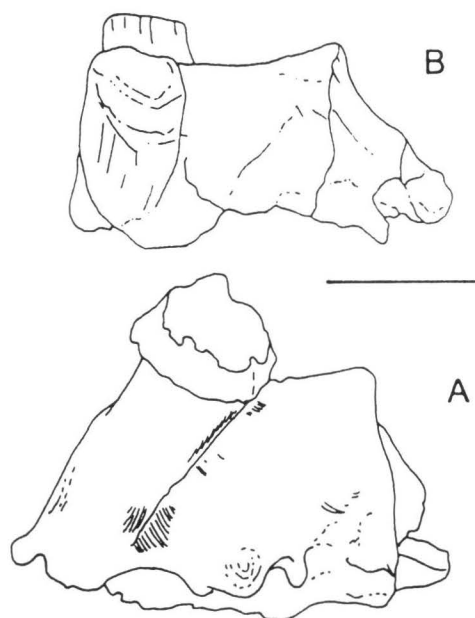
Text-fig. 5 - The regression of basal tines and the change of the orientation of the antlers in *Megaceroides*, is shown. A) *M. obscurus*, lectotype from Cromer-Forest bed Formation; B) *M. verticornis* from Süssenborn (Kahlke, 1956, redrawn and reversed; C) *M. dawkinsi*, Cromer-Forest bed Formation (Azzaroli, 1953, redrawn); D) *M. solilhacus*, lectotype from Solilhac (Azzaroli, 1979, redrawn); E) *M. solilhacus*, Isernia (IS22026); F) *M. algericus*, from Phacochères, Algeria (Hadjouis, 1990, redrawn).

poorly known, it would appear that digital terminations on the edge of the palmation are characteristic of *M. solilhacus* from the type locality and from Terranera, while they do not occur on the palmations of *M. verticornis*. With regards to the other shared characteristics, the labial groove of the fourth lower premolar is highly variable (cf. Menéndez, 1987) within the genus, while the slight pachyostosis is a primitive character, and is therefore of little significance for the determination of phylogenetic relationships; moreover, it varies with the age of the individual, as Lister (1994) demonstrates for *Megaloceros giganteus*. Size, finally, is strongly influenced by environmental conditions, and is therefore variable.

If one examines only the *M. solilhacus* specimens

from the type locality, the most significant diagnostic characteristics are those observable in the proximal section of the antlers, in other words the absence of the spurious tine, the reduction of the outer tine, the shortening of the horizontal part of the beam, and its tendency to be flattened starting at the anterior tine. The *M. sp.* from Voigtstetd, Süssenborn, and Mosbach could therefore either belong to *M. verticornis*, as suggested by Geraads (1986), or be a distinct, closely related species.

The fossil from Venta Micena, (Menéndez, 1987) agrees with *M. solilhacus* in the morphology of the proximal part of the antler (i.e. lack of basal tines), but differs for the distinctly smaller braincase, for some plesiomorphic characters, such as the more elongated parietal roof and the different directing



Text-fig. 6 - Comparison between A) the skull of *M. solilhacus* from Blanzac (Azzaroli, 1979, redrawn), and B) the skull from Venta Micena (Menéndez, 1987, redrawn and reversed). The scale is 10 cm.

pedicles of the antlers (Text-fig. 6), and for the slender limb bones. Given also that the age of this deer is distinctively older than that of the other specimens of *M. solilhacus* finds, we are inclined to consider this form as a closely related, but distinct species from *M. solilhacus*. Therefore we propose to indicate this form with the name *M. aff. solilhacus*, to stress the necessity of its sistematical revision.

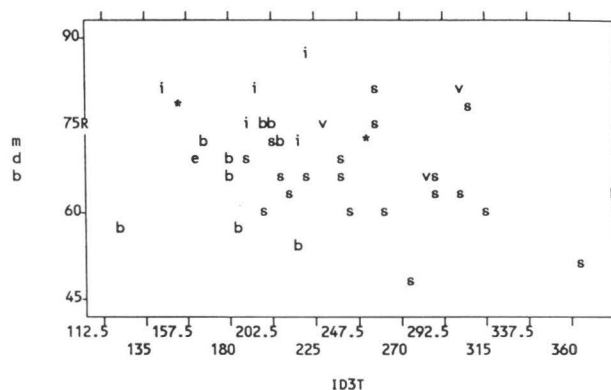
The megalocerine from Akhalkalaki, which is characterized by long, slender metapodials, could be closely related to the Venta Micena form, even though it is difficult to assess, because it is known only from a mandible and some post-cranial elements.

Finally, we can suggest the possibility that the French form from Montreuil, described by Pohlig (1892) as «*Cervus*» *belgrandi* and referred by Kahlke (1956-59) to *M. verticornis*, may be conspecific with *M. solilhacus*, even though the few remains published make a final attribution impossible.

Morphometric analysis of the antlers

Some of the differences between the antlers of *M. solilhacus* and *M. verticornis* listed above have been confirmed by bivariate and multivariate analyses of the remains.

The shortening of the horizontal section of the beam in the specimens from Isernia is confirmed in Text-fig. 7, where the index which relates the distance between the anterior tine and the burr to the



Text-fig. 7 - Scatter diagram of ID3T index against minimum diameter of burr (mdb) in *Megaceroides*.

Legend: i = *Megaceroides solilhacus*, Isernia. * = *M. verticornis*, Cromer Forest bed Formation. b = *M. dawkinsi* Cromer Forest bed Formation. e = *M. solilhacus*, Venta Micena. v = *M. verticornis*, Voigtstedt. s = *M. verticornis*, Süssenborn.

maximum diameter of the burr ($ID3T = \text{diat-b} / \text{maxdb} \times 100$) is compared with the minimum diameter of the burr. The Isernia population plots in the lower range of the field of variability, like *M. dawkinsi* from Cromer Forest bed formation. The *M. aff. solilhacus* from Venta Micena occupies a position that corresponds to a low ID3T value (symbol e). Also, the ID3T index of the antler selected by Azzaroli (1979) as the lectotype of *solilhacus* is 175, a value that falls within the range of the Isernia megalocerine and *M. dawkinsi*.

The results of a comparison between the ID3T index and the angle formed between the plane of the burr and the axis of the beam, a measurement indicating the orientation of the antler with respect to the skull, are also interesting. In the populations of Isernia and in *M. dawkinsi* from the English localities, this angle falls within a well defined range, between 60° and 70°, and in Text-fig. 8 the specimens make up a group that is quite distinct from *M. verticornis*. Moreover, it is worth to note that the specimens within every sample tend to cluster in subgroups, suggesting an influence of the ontogenetic development of antler on ID3T index. This pattern is in particular evident in the large population from Süssenborn.

In addition, a principal component analysis based on 8 measurements of the section of the beam between the burr and the anterior tine (Tab. 7), was carried out on the antlers of *Megaceroides solilhacus* from Isernia, *Megaceroides verticornis* from Süssenborn and Voigtstedt, and *Megaceroides dawkinsi* from Cromer Forest bed. The descriptive statistics of the variables are given in Tab. 8. The first two factors,

MAXDB	= Maximum diameter burr
MINDB	= Minimum diameter burr
MAXDBAB	= Maximum diameter beam above burr
MINDBAB	= Minimum diameter beam above burr
MAXDBA2	= Maximum diameter beam above 2nd tine
MINDBA2	= Minimum diameter beam above 2nd tine
3TBD	= Distance of basal end of 3rd tine from the burr
ANGLE	= Angle formed between plane of burr and axis of beam

Tab. 7 - Measurements of the antlers used for the analysis of the principal components.

which account for 84% of the total variance, were selected. The first factor (66.1%) is influenced by the diameters of the beam, and in particular its maximum and minimum diameters above the burr. The second factor which accounts for 18.3% is influenced by the distance between the anterior tine and the burr, and by the angle between the plane of the burr and the axis of the beam, and therefore expresses the morphology of the antler.

The results of this analysis are shown in Text-fig. 9. In Text-fig. 9b the scatter diagram between the first and the second principal components (PC1 and PC2), highlights that *M. dawkinsi* from the English localities and *M. solilhacus* from Isernia share a morphological affinity, as is revealed by the distribution of the specimens with respect to the axis of the second factor. The megalocерine remains from Voigtstetd fall within the high values of the range of variation of the *M. verticornis* from Süssenborn, thus confirming its fairly large size.

Finally, we must discuss the distribution of the samples that make up the Süssenborn population. The dispersion observable on the ordinate (size factor) is apparently due to the inclusion of individuals that were not fully grown. On the other hand, the

Initial Statistics:

Variable	Communality	* Factor	Eigenvalue	Pct of Var	Cum Pct
MAXDB	1.00000	* 1	5.29022	66.1	66.1
MINDB	1.00000	* 2	1.46124	18.3	84.4
MAXDBAB	1.00000	* 3	.38579	4.8	89.2
MINDBAB	1.00000	* 4	.32137	4.0	93.2
MAXDBA2	1.00000	* 5	.23995	3.0	96.2
MINDBA2	1.00000	* 6	.16911	2.1	98.3
3TBD	1.00000	* 7	.08866	1.1	99.5
ANGLE	1.00000	* 8	.04367	.5	100.0

	FACTOR 1	FACTOR 2
MAXDB	.91971	-.05236
MINDB	.89257	-.17257
MAXDBAB	.94896	.10117
MINDBAB	.93065	-.18472
MAXDBA2	.88521	-.00634
MINDBA2	.87433	.11581
3TBD	.53009	.73592
ANGLE	-.22803	.91067

Tab. 8 - Descriptive statistics of the variables used in the analysis of the principal components.

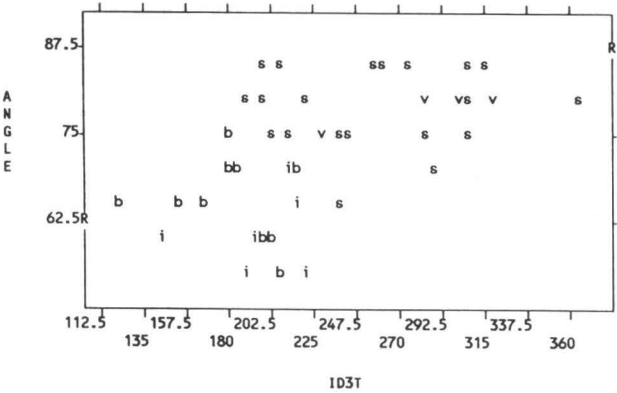
dispersion observable for the second factor is also probably attributable to the inclusion of individuals belonging to populations from different stratigraphic levels in the Süssenborn sample. Therefore, the dispersion is not just an expression of the individual variability within a single population, but may as well be attributable to morphological changes of an evolutionary nature.

Subfamily CERVINAE Baird, 1857
Tribe CERVINI Viret, 1961
Genus CERVUS Linneus, 1758

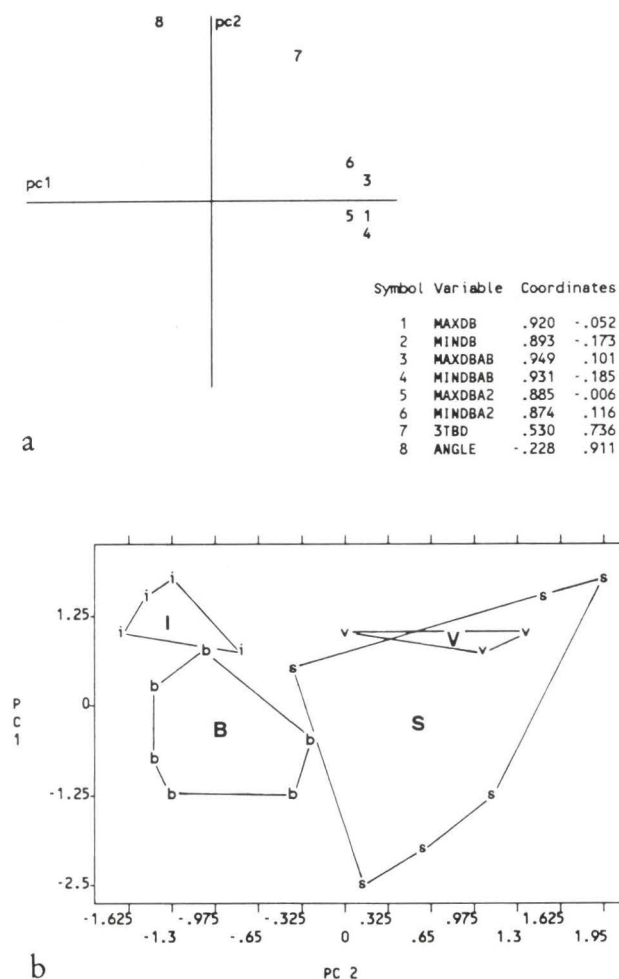
CERVUS ELAPHUS cf. C. e. ACORONATUS Beninde, 1937
Text-fig. 10

Material

Antlers: IS2612 - basal portion of antler.
Dentition: IS2551 - right M2/; IS2554 - left M3/; IS2555 - right M/2; IS2556 - right M/2; IS2560 - fragment of right M/3; IS2561 - fragment of upper molar; IS2562 - fragment of upper molar; IS2563 - fragment of M2/; IS2564 - I/1
Post-cranial elements: IS2601 - I phalange; IS2602 - II phalange; IS12 - proximal epiphysis of right metacarpus; IS2603 (=4) - distal epiphysis of metacarpus; IS1 - fragment of right calcaneus; IS2608 - right cubonavicular.



Text-fig. 8 - Scatter diagram of ID3T index against the angle formed between the plane of burr and the axis of beam in *Megaceroides*. Symbols as in Text-fig. 7.



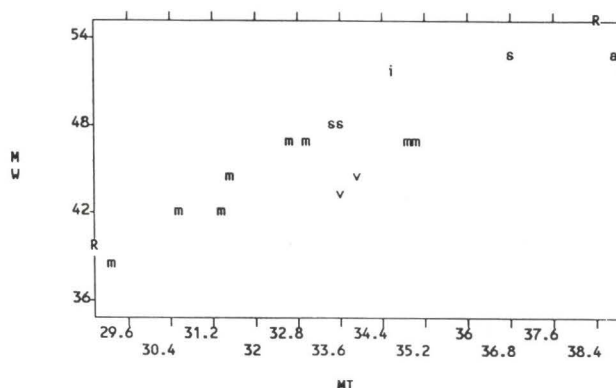
Text-fig. 9 - a) Loadings of PC1 and PC2. b) Factor scores scatter diagram. The lines indicate the area of dispersion of the samples, the symbols correspond to the mean values of the samples.
 Legend: i = *Megaceroides solilhacus*, Isernia. b = *M. dawkinsi* Cromer Forest bed Formation. v = *M. verticornis*, Voigtstedt. s = *M. verticornis*, Süssenborn.

Description and comparisons

The presence of *C. elaphus* in the Isernia deposits is indicated by an antler fragment in which the attachments of the brow and bez tines are preserved, and by the size of dental and postcranial elements. The attribution to the subspecies *acoronatus* cannot be demonstrated, though it is suggested by the stratigraphic position of the find. The dimensions (Tab. 9; Text-fig. 10) and the morphology of the remains (e.g. the brachyodont teeth) are comparable with the specimens found in other localities that are referable to the same subspecies (e.g. Süssenborn, Mosbach).

Sample	OL	NL	W	H
M2\ IS2551	*24.0	24.0	25.9	13.3
M2\ IS2563	23.5	*21.0	*26.0	*14.0
M3\ IS2554	22.8	22.2	24.5	12.9
M/2 IS2555	23.5	22.4	14.9	7.8
M/1 IS2556	22.9	20.1	13.0	11.8
M/1 IS2559	20.7	20.0	12.3	*13.0

Tab. 9 - Teeth of *Cervus elaphus* cf. *C. e. acoronatus* from Isernia. Measurements in mm. * indicates inferred values.
 Legend: OL = Occlusal length. NL = Neck length.
 W = Maximum width. H = Height of the crown.



Text-fig. 10 - Scatter diagram of maximum thickness (MT) against the maximum width of proximal epiphysis of metacarpus (MW) in *Cervus elaphus acoronatus*.
 Legend: i = *Cervus elaphus* cf. *C. e. acoronatus*, Isernia. m = *C. elaphus acoronatus*, Mosbach. v = *C. elaphus acoronatus*, Voigtstedt. s = *C. elaphus acoronatus*, Süssenborn. a = *C. elaphus acoronatus*, Atapuerca (data from Azanza & Sanchez, 1990).

Subfamily CERVINAE Baird, 1857
 Tribe CERVINI Viret, 1961
 Genus DAMA Frisch, 1775

DAMA cf. D. CLACTONIANA (Falconer, 1886)
 Text-fig. 12

Material

Antlers: IS20657 - right antler with forehead
 Dentitions: IS2566 - left M3/; IS2567 - right M3/;
 IS2568 - left M1/; IS2569 - fragment of right M2/;
 IS2570 - right P4/; IS2571 - left M/2; IS2572 - right M1/; IS2562 - I/2.

Post-cranial elements: IS2573 - left cubo-navicular; IS2574 - distal portion of humerus; IS2575

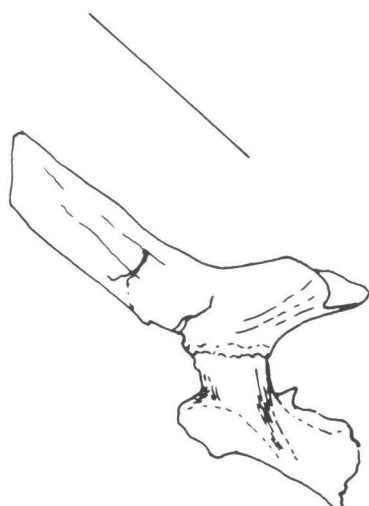
- distal portion of humerus; IS2576 - distal fragment of I phalange; IS2604 - left metacarpus; IS2613 - distal fragment of left tibia.

Description and comparison

The presence of the genus *Dama* is revealed by a proximal fragment of an antler in which the insertion of the basal tine is preserved (Text-fig. 11). This tine branches off immediately above the burr, and its basal diameter is comparable to that of the beam, with which it forms an angle of about 125°. Other morphological characters revealed by the post-cranial elements (e.g. metacarpal) confirm this generic attribution. Lister (1990) has identified a series of characters that serve to distinguish between *Cervus* and *Dama*. In the proximal metacarpal, for example, the articular facets are separated by a caudally located groove in *Cervus elaphus*, and are welded in *Dama*; the latter feature is observable in the Isernia specimen.

The measurements of teeth are reported in Tab. 10.

The metacarpal (IS2604) and the distal fragment of a tibia (IS2613) are fairly large. The metacarpal (Text-fig.12), is considerably larger than those of *Pseudodama* from the upper part of the Late Villafranchian (e.g. *P. farnetensis* from Selvella, and *P. sp.* from Cava dell' Erba), or those of the middle-late Pleistocene (e.g. *Dama sp.* from S. Sidero 3; Riss-Würm interglacial or first Würm interstadial; De Giuli, 1983) and recent populations of *Dama dama*, while it is close to the range of size variation of the



Text-fig. 11 - Antler with part of forehead of *Dama cf. D. clactoniana* (IS 20657) from Isernia. The scale is 10 cm.

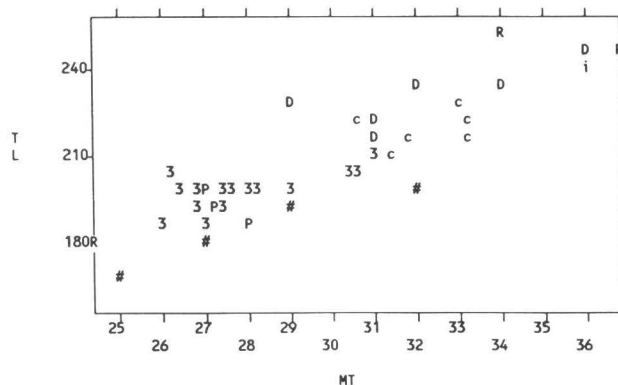
Sample	OL	NL	W	H
M3\ IS2566	19.1	18.3	21.5	9.2
M3\ IS2567	19.6	19.3	21.1	12.1
M1\ IS2568	17.8	16.6	19.1	8.8
M2\ IS2569	19.3	*18.0	*20.0	*10
P4\ IS2570	11.7	11.5	16.2	16.6
M/2 IS2571	19.5	18.2	10.7	12.2

Tab. 10 - Teeth of *Dama cf. D. clactoniana*. Measurements in mm.

Legend: OL = Occlusal length. NL = Neck length. W = Maximum width. H = Height of the crown.

Dama clactoniana found in English middle Pleistocene localities (Clacton, Swanscombe) and at Riano (cf. Leonardi & Petronio, 1976). The tibia (Tab. 11) fall within the variation range of *Dama clactoniana* from Riano (articular width of distal epiphysis: max = 44 mm, min = 30 mm, average = 34.9 mm; articular thickness of the distal epiphysis: max = 37 mm, min = 25 mm, average = 28.06 mm; Leonardi & Petronio, 1976). The morphology of the proximal fragment of the antler, with a very massive ocular tine, is also observable in *D. clactoniana*.

Even though the lack of a representative sample of antlers did not allow us to observe other diagnostic characters of the species *clactoniana*, for example the incompletely developed palmation or the third accessory tine, the large size and the mor-



Text-fig. 12 - Scatter diagram of maximum thickness of distal epiphysis (MT) against total length of metacarpal (TL) in *Pseudodama* and *Dama*.

Legend: i = *Dama cf. D. clactoniana*, Isernia. R = *D. clactoniana*, Riano (data from Leonardi & Petronio, 1976). D = *D. clactoniana*, from Swanscomb, Clacton (data from Leonardi & Petronio, 1976). c = *Pseudodama farnetensis*, Selvella (Val di Chiana). P = *Pseudodama sp.*, Cava Pirro-Cava Dell'Erba (Foggia, South Italy). 3 = *Dama sp.* San Sidero 3, (Lecce, South Italy). # = *Dama dama*, attuale (Museo di Storia Naturale «La Specola», Firenze).

Sample	1	2	3	4	5
IS2613	40.3	38.3	31.6	33.2	*30

Tab. 11 - Tibia of *Dama* cf. *D. clactoniana*. Measurements in mm.

Legend: 1 - Maximum width of the distal epiphysis. 2 - Articular width of the distal epiphysis. 3 - Width of the troclea at the distal epiphysis. 4 - Thickness of the distal epiphysis. 5 - Articular thickness of the distal epiphysis.

phology of the basal tine are sufficient for a fairly precise systematic attribution.

Biochronological range and systematical remarks regarding Dama clactoniana

In Italy, *Dama clactoniana* was present for much of the middle Pleistocene. A rich sample has been found at Riano (Leonardi & Petronio, 1976), and many specimens have been recovered from other sites in Latium that record the first extrusive activity of the Sabatine and Albano volcanic complexes (cf. Caloi & Palombo, 1986). At Fontana Ranuccio (radiometric age of 0.458 ± 0.0057 Ma), for example, this species is associated with *Megaceroides verticornis*. It has also been reported from Cava Pompei (Latium, cfr. Guidi & Piperno, 1992), Notarchirico (Venosa basin, about 500,000 years; Belli *et al.*, 1991), and recently from the Cesi locality in the Colfiorito Basin (Ficcarelli *et al.*, in progress). This species seems disappear from the assemblages of the middle Pleistocene at a time that follow the oxygen stage 7, since one of its last occurrences is at Sedia del Diavolo (Riss II - III interstadial; Caloi *et al.*, 1980; Caloi & Palombo, 1986; Gliozzi *et al.*, 1995), which has been correlated to this stage of the isotope stratigraphy. In this phase, however, the faunal assemblage already contained a true fallow deer with primitive characteristics, which seems to have coexisted with the clactonian form (Gliozzi *et al.*, 1995). The many reported occurrences of the species *clactoniana* in European middle Pleistocene localities (England, France, Spain) show how widely dispersed this form became over this interval of time.

Subfamily ODOCOILEINAE Pocock 1923

Tribe CAPREOLINI Simpson 1945

Genus CAPREOLUS Gray 1821

CAPREOLUS sp.

Material

Dentition: ISNN - right M/1.

Post-cranial elements: IS2609 - fragment of left humerus; IS9 - I phalange.

Description

On the basis of their small size and on the morphology, the remains are attributable to *Capreolus*, though their small number makes further conclusions impossible.

CONCLUSIONS

The examination of the remains of deer from Isernia has revealed a well diversified assemblage.

The occurrences of *Cervus elaphus* cf. *C. e. acoronatus* and *Capreolus* sp. do not contribute new systematic insights, in part because of the scantiness of the material, nor do they allow particular biochronological conclusions to be drawn. On the other hand, the presence of *Megaceroides solilhacus* and *Dama* cf. *D. clactoniana* are interesting. The study of the megalocerine specimens from Isernia, which display a certain degree of morphological consistency with regards to the proximal part of the antler, has allowed us to a better determination of the diagnostic characteristics for *M. solilhacus*, and thus constrain its range of variation. The lineage of *M. solilhacus* first occurred in Europe in the late part of early Pleistocene (*M. aff. solilhacus* from Venta Micena, Spain), and for much of the middle Pleistocene occupied a widespread geographic range, which overlapped the considerably better known range of *M. verticornis*. *M. solilhacus* represents a phyletic lineage distinct from, though closely related to, *M. verticornis*. To date, in Italy, *M. solilhacus* has been reported from central and southern localities (Latium, Colfiorito Basin, several sites around Venosa). Its dispersal could be indicative of a tendentially open landscape, as the occurrence at Isernia of other faunal elements like *Elephas*, *Bison* and *Stephanorhinus*, suggest.

Despite the numerous reported findings, *Dama clactoniana* is not yet well described, and, most importantly, its relationship with *Dama dama* is not yet clear. Moreover, the systematics and chronological distribution of the medium sized deer in the middle Pleistocene is further complicated by the fact that some students quote the occurrence, throughout the Galerian, of forms attributable to the genus *Pseudodama* (Di Stefano, 1994).

ACKNOWLEDGEMENTS

The study of deer material from Isernia La Pineta site has been carried on thanks to Prof. B. Sala (Ferrara University) to whom we are deeply obliged.

- from early Pliocene to late Pleistocene. Poster presentato al Convegno INQUA, 3-10 August 1995, Berlin.
- GUIDI, A. & PIPERNO, M., 1992, Italia preistorica. Editori Laterza, 685 pp, Bari.
- HADJOUIS, D., 1990, *Megaceroides algericus* (Lydekker, 1890) du gisement des Phacochères (Alger, Algérie). Etude critique de la position systematique de *Megaceroides*: Quaternaire, 3-4: 247-258.
- JOLEAUD, L., 1916, *Cervus (Megaceroides) algericus* Lydekker: Rec. et Not. de la Soc. Archéol. de Costantine, 66: 1-67.
- KAHLKE, H.D., 1956-1959, Die Cervidenreste aus den Altpleistozänen Ilmkiesen von Süssenborn bei Weimar. Akad. Verlag, I, II, III.
- , 1958, Die Cervidenreste aus den Altpleistozänen tonen von Voigtstedt bei Saugerhausen: Akad. Verlag, Die Shadel, Gewerde und Gehorne, I, 51 pp.
- , 1960, Die Cervidenreste aus den Altpleistozänen Sanden von Mosbach (Blebrich-Wiesbaden): Akad. Verlag, Die Gewerde, Gehorne und Gebisse, 1: 1-75.
- , 1965, Die Cervidenreste aus dem Tonen von Voigtstedt in Thüringen. Paläont. Abh. A, 2 (2/3): 381-424.
- , 1969, Die Cerviden-Reste aus den Kiesen von Süssenborn bei Weimar; Paläont. Abh. A, 3 (3/4): 547-609.
- KOENIGSWALD, W. VON & TOBIEN, H., 1987, Bemerkungen zur Alterstellung der pleistozänen Mosbach- Sande bei Wiesbaden: Geol. Jb. Hessen, 115 (2): 227-237.
- KOTSAKIS, T., ESU, D. & GIROTTI, O., 1992, A post-Villafranchian cold event in central Italy testified by continental Molluscs and Rodents: Boll. Soc. Geol. It., 111 (2): 335-340.
- LEONARDI, G., & PETRONIO, C., 1976, The fallow deer of european Pleistocene: Geologica Romana, 25:1- 67, Roma.
- LISTER, A.M., 1986, New results on Deer from Swanwanscombe, and stratigraphical significance of Deer in the middle and upper Pleistocene of Europe: Jour. of Arch. Sc., 13: 319-338.
- , 1990, Critical reappraisal of the Middle Pleistocene deer species *Cervus elaphoides* Kahlke: Quaternaire, 1 (3-4): 175-192.
- , 1994, The evolution of the giant deer, *Megaloceros giganteus* (Blumenbach): Zool. Journ. Linn. Soc., 112: 65-100.
- , MCGLADE, J.M. & STUART, A.J., 1990, The early middle Pleistocene vertebrate fauna from Little Oakley, Essex: Phil. Trans. R. Soc. Lond., B 328: 359-385.
- MAZZA, P., 1996, New evidence on the Pleistocene Hippopotamuses of Western Europe: Geologica Romana, 31: 61-241 (1995).
- MCPHERRON, A. & SCHMIDT, V., 1983, Paleomagnetic dating at Isernia La Pineta. In AA. VV., «Isernia La Pineta, un accampamento più antico di 700.000 anni», Catalogo della mostra, ed. Calderini: 49-62.
- MELENTIS, J.K., 1967, Studien über fossile vertebraten Griechenlands. *Orthogonoceros verticornis* aus dem Altpleistozän des Beckens von Aliakmon (Griechenland): Ann. Geol. Pays Helleniques, I s., 17: 447-454.
- MENÉNDEZ, E., 1987, Cérvidos del Yacimiento del Pleistoceno inferior de Venta Micena-2, Orce (Granada, España): Paleont. I Evol., Mem Esp., 1: 129-180.
- MONTEZEMOLO, C.G., 1964, Les fouilles dans le bassin fluvio-lacustre de Venosa (Potenza, Italia): Rep. 6th Intern. INQUA Congr., Warsaw 1961, 2: 217-525.
- MOULLADE, E., 1886, Note sur une nouvelle espèce de daim fossile: Mem. Soc. Agr. Sci. H.te Loire, 4: 304-306.
- MOYA-SOLA, S. & MENÉNDEZ, E., 1986, Los Artiodáctilos (Bovidae y Cervidae, Mammalia) del Pleistoceno inferior de Europa occidental: ensayo de síntesis: Paleont. I Evol., 20: 289-295.
- POHLIG, H., 1892, Cerviden des Thüringischen Diluvial-Travertines mit Beiträgen über andere diluviale und über recente Hirschformen: Paleontog., 39:215-261.
- RADULESCO, C. & SAMSON, P., 1967, Sur un nouveau Cerf mégacérin du Pleistocène moyen de la depression de Brasov (Roumanie): Geologica Romana, 6: 317-344.
- ROBERT, F., 1829, Mémoire sur les ossements fossiles des environs de Cussac, Commune de Polignac (H.te Loire): Mém. Soc. Agr. du Puy, 2: 68-88.
- SALA, B., 1983, La fauna del giacimento di Isernia La Pineta (nota preliminare). In AA.VV., «Isernia La Pineta: un accampamento più antico di 700.000 anni». Catalogo della omonima mostra, Museo Nazionale di Isernia, Bologna, Calderini editore: 71-79.
- , 1987, *Bison schoetensacki* Freud. from Isernia La Pineta (early Mid-Pleistocene-Italy) and revision of the European species of bison: Palaeontogr. Ital., 74 (1986): 113-170.
- , 1990, *Panthera leo fossilis* (v. Reich., 1906) (Felidae) de Isernia la Pineta (Pléistocène moyen inférieur d'Italie): Geobios, 23 (2): 189-194.
- , MASINI, F., FICCARELLI, G. & TORRE, D., 1992, Mammal dispersal events in the Middle and Late Pleistocene of Italy and Western Europe: Courier Forsch.-Inst. Senckenberg, 153: 59-68.
- , & FORTELIUS, M., 1993, The rhinoceroses of Isernia La Pineta-early Middle Pleistocene: Palaeontogr. Ital., 80: 157-174.
- SEVINK, J., HEBEDA, E.H., PRIEM, H.N.A. & VERSHURE, R.H., 1981, A note on approximately 730.000- year-old manual fauna and associated human activity site near Isernia, central Italy: Journ. Archaeol. Sc., 8: 105 pp..
- THOUVENY, N. & BONIFAY, E., 1984, New chronological data on European Plio-Pleistocene faunas and hominid occupation sites: Nature, 308 (22): 355-358.
- TOULA, VON F., 1902, Das Nashorn von Hundsheim. *Rhinoceros (Ceratobhinus Osborn) hundsheimensis* nov. form: Abh. K.K. Geol. Reich., 19:92 pp.
- TOZZI, C., 1969, Segnalazioni di una grotta con fauna fossile a Borgio (Savona): Atti Soc. Tosc. Sc. Nat., Mem., A, 76: 195-208.
- VEKUA, A.K., 1986, The Lower Pleistocene Fauna of Mammals of Akhalkalaki (Southern Georgia, USSR): Palaeontogr. Ital., 74: 63-96.
- VISLOBOKOVA, I., 1990, The fossil deer of Eurasia: Trudy Paleont. Inst., 240: 208 pp. In russian.

(manuscript received July 31, 1995
accepted September 30, 1996)

Laura ABBAZZI

Dipartimento di Scienze della Terra
Università di Firenze
Via G. La Pira 4, 50121 Firenze, Italy

Federico MASINI

Dipartimento di Geologia e Geodesia
Università di Palermo
Corso Tukory 131, 90134 Palermo, Italy