

<i>Bollettino della Società Paleontologica Italiana</i>	38 (1), 1999	ISSN 0375-7633	109-119	1 pl.	Modena, Maggio 1999
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The elephant *Archidiskodon meridionalis* (Nesti, 1825) from the Lower Pleistocene of Steggio (Possagno, Treviso, north-east Italy)

Paolo REGGIANI

Piove di Sacco
Padova, Italy

KEY WORDS – Elephantidae, Systematics, Lower Pleistocene, Possagno (Treviso), N-E Italy.

SUMMARY – During the last season of excavations carried out in 1993, the fossil beds at Steggio (Possagno, Treviso) yielded many fossil bones including various elephant remains. Lithologically, the Steggio succession belongs to a unit informally known as the "Argille di Steggio", composed of clayey layers alternate with gravelly layers. The elephant bones found at Steggio mainly belong to juvenile individuals. The biometric values of the molars fall within the range attributed to *Archidiskodon meridionalis*. The examination of the carpals and comparisons with the material found at Pietrafitta and in the Valdarno made it possible to highlight some of the typical characteristics of this species.

RIASSUNTO – [L'elefante *Archidiskodon meridionalis* (Nesti, 1825) del Pleistocene inferiore di Steggio (Possagno, Treviso, Italia nord-orientale)] – Nel giacimento fossilifero di Steggio (Possagno, Treviso), durante l'ultima campagna di scavo, condotta nel 1993, furono recuperati molti reperti osteologici fossili, fra i quali diversi resti di elefante. Da un punto di vista litologico i reperti osteologici sono contenuti in una successione stratigrafica definita informalmente "Argille di Steggio", costituita da strati argillosi alternati a strati ghiaiosi. Fra i reperti vi sono resti di elefante pertinenti ad esemplari giovani. I valori biometrici dei molari rientrano nella gamma attribuita ad *Archidiskodon meridionalis*. L'esame dei carpali e la comparazione con il materiale scoperto a Pietrafitta e nel Valdarno ha permesso di evidenziare alcune caratteristiche tipiche di questa specie.

FOREWORD

The taxonomy of the group of elephants which appeared in Europe in the late Pliocene and disappeared in the Holocene is still debated. Some authors prefer to use the name *Mammuthus* Burnett, 1830 to indicate a group of Eurasian elephants, including *Archidiskodon meridionalis*, which appeared in the late Pliocene and disappeared in the Holocene (Aguirre, 1968, 1995; Beden, 1986; Lister, 1996; Maglio, 1973 and others). On the other hand, others think that it is more appropriate to use the name *Archidiskodon*, created by Pohlig in 1885, to indicate primitive elephants which are different from those belonging to the genus *Mammuthus* (Azzaroli, 1977; Dubrovo, 1975, 1985, 1990; Foronova, 1986; Garutt, 1995, 1998; Garutt & Bajguseva, 1981; Guenther, 1986 and others). Hence there are two different taxonomic interpretations. Lister (1996) prefers to group all the species in the only genus *Mammuthus*, but he also stated that the genus *Archidiskodon* is nomenclatorially available in the sense of the International Code of Zoological Nomenclature. I think that the remarkable differences between *Mammuthus* and *Archidiskodon* - cranial, lower jaws, dental characteristics and some carpal bones - are sufficient to keep these two genera distinct. As a matter of fact, the cranial, mandibular and dental characteristics in present mammals, are particularly important to distinguish the genera belonging to the same family.

The terminology used in this report to distinguish features of elephantid dentition is suggested by Aguirre (1968), Maglio (1973) and Lister (1996).

Since the finds include well preserved autopodial bones which are rarely described in the literature, we found appropriate to include a comparative description of the bones of *A. meridionalis* and those of *Palaeoloxodon namadicus* and *Palaeoloxodon antiquus*.

INTRODUCTION

The Steggio area is in the west of Possagno (Treviso province), at the foot of the impressive mountain ridge in the group Cima della Mandria-Monte Pallon-Monte Tomba. The stratigraphic succession is alternately made of clays, slime, sand and lignitic levels with gravel, unlike the sediments of the Possagno Marl (Paronuzzi & Tonon, 1992; Ghiotto, 1995).

The Quaternary lacustrine site at Steggio was discovered in 1986 when a fragment of a fossil tibia was found during work on a landslide (Tonon, 1994). In the following four seasons of excavation, directed by Tonon, then director of the Science Museum at Pordenone, many bone remains were found belonging to various animal species as well as abundant vegetal remains, including some large sized trunks (Ghiotto, 1995). The geomorphological study of the lake basin resulted in two publications (Paronuzzi & Tonon, 1992; Paronuzzi, 1993), while the numerous

bone remains and have been partially published in Sala & Tonon (1992).

In this paper the elephant bones are examined. These bones, and in general all the fossil vertebrates, were found during the excavation of a particularly vast area which led to the removal of about 40,000 cubic metres of sediment. Although the bones were not found in anatomical connection, some of the autopodial bones seem to belong to animals of a similar size if not to the same individual. In fact three metacarpals (II mc. n. 159/c, III mc. n. 181, IV mc. n. 314) and two carpals (magnum n. 203 and lunar n. 214) articulate perfectly together. Moreover, many of the fossil bones have perfectly preserved surfaces, without traces of erosion, and therefore it is likely that they have not been transported over a long distance.

Only a preliminary and partial list is given for the many fossil bones belonging to other taxa, since these have not yet been studied. The most abundant remains appertain to *Stephanorhinus etruscus* and a large unidentified bovid; an antler belonging to *Eucladoceros cf. senezensis* (Sala & Tonon, 1992) and a few other bones of a small sized deer were also found. Carnivores are represented by a hemimandible and two molars of *Ursus etruscus* (Sala, pers. comm.). The soil sieving also led to the retrieval of some rodent teeth.

The elephant bones from Steggio have been directly compared with the abundant bones of *Archidiskodon meridionalis* found at Pietrafitta (Umbria), attributed to the association of the Farneta Faunal Unit of the latest Villafranchian (Torre *et al.*, 1992; Gentili *et al.*, 1996), and from Valdarno (Tuscany), and with the numerous bones from Castel di Guido (Lazio) attributed to *Palaeoloxodon namadicus* of the first Post-Galerian (Sala & Barbi, 1996). In addition, abundant published material was also taken into consideration which will be referred to in the text.

ANATOMICAL DESCRIPTION

The terminology proposed by Osborn (1942) is used to describe the premolars and molars, whereby the jugal teeth are listed in order of eruption, from the first to the sixth: Dp2, Dp3, Dp4, M1, M2, M3.

A brief description follows of the main biometric parameters taken into consideration regarding the elephant molars (all the measurements in the table are expressed in millimetres):

- Number of laminae, the total number of laminae which make up the molar, excluding the first and the last lamella (talons), indicated in the table with an x.
- Total length of the crown measured parallel to the longitudinal axis of the tooth
- Maximum width of the crown including the cement, measured perpendicularly to the median axis of the laminae
- Maximum height of the crown, from the neck to the top of the highest lamina

- Lamellar frequency, the number of laminae in a 10 cm long area, it is the medium value of four measures calculated on the sides of the molar (labial and lingual, top and bottom)

- Average thickness of the enamel, measured on the occlusal surface of the molar and calculated following the method proposed by Aguirre (1968). The highest and lowest values are indicated in brackets.

- Length-number of laminae quotient (LLQ), the relationship between the length and the number of laminae, calculated in the central part of the molar

- Cooke's hypsodonty index, the percentage relationship between the height of the highest lamina and the maximum width of the crown, including the cement

- Meiring's hypsodonty index, the percentage relationship between the maximum width and the maximum height of the crown (Aguirre, 1968).

M² (n. 244/d)

The first four laminae and the anterior talon are preserved in this germinal molar. The height of the crown along with its width makes one think that it is a second superior molar. The tooth in question was not in use when the animal died, and in fact the cement around the laminae had not yet formed and none of the laminar digitations show signs of use wear. The laminae have 5 or 6 well separated digitations.

The quite high lamellar frequency is probably due to the incomplete development of the cement between the laminae. The same lamellar frequency was found in some M₃ and M₂ (n. 386, 389, 390, 379) from Pietrafitta which had also not been used.

Steggio	
Length of the fragment	92
Width of the crown	82 (IV lamina)
Height of the crown	126 (IV lamina)
Number of laminae	x 4 -
Lamellar frequency	6
LLQ	17

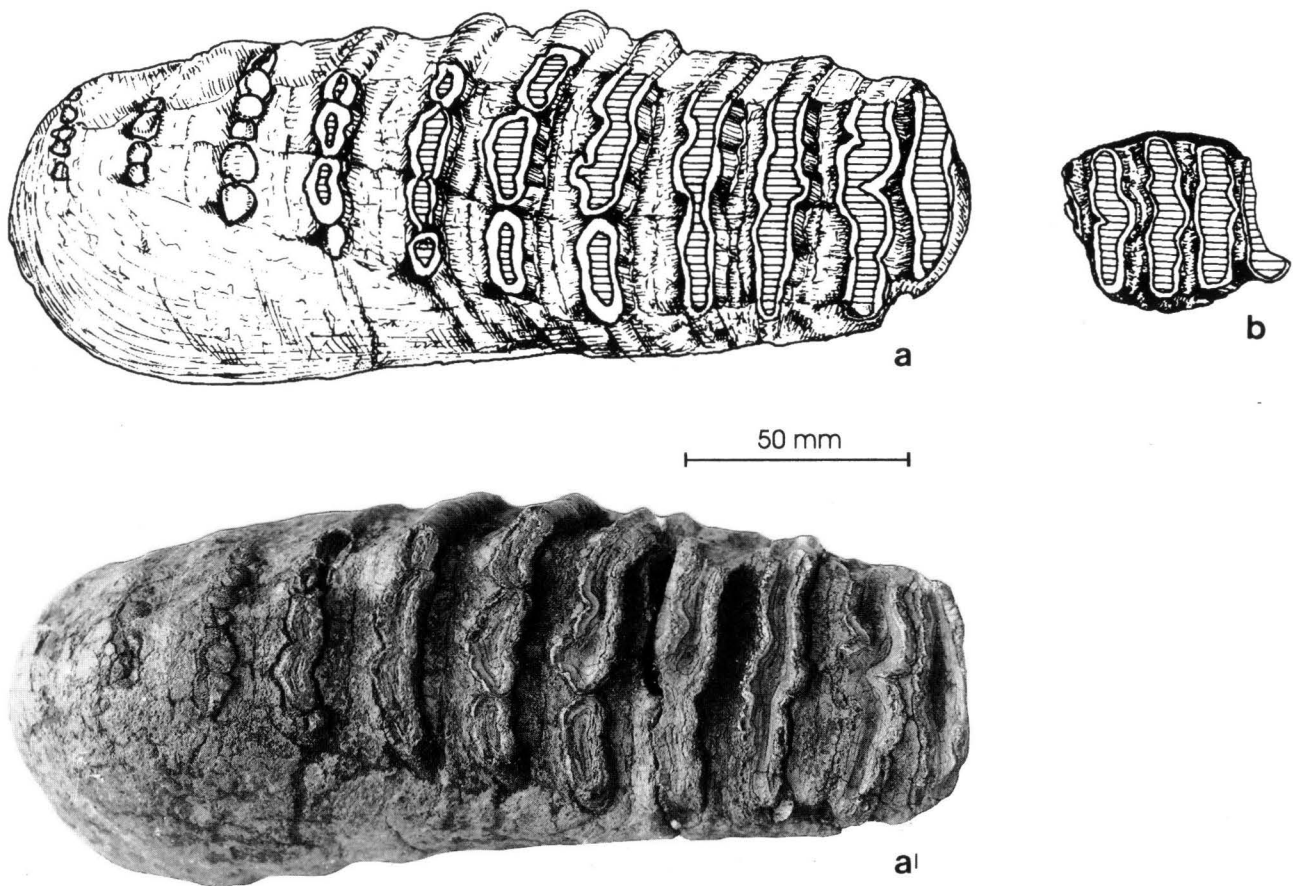
Tab. 1 - Measurements of M² (n. 244/d)

Right Dp₃ (n. 305)

It is very well preserved and characterised by a long root. The enamel on the laminae is black while the cement and the dentine are light brown in colour. According to Azzaroli (1949), the dark colour of the enamel is indicative of fossilisation in a sub-aqueous environment.

The front lamina is completely worn in viewed occlusal (Text-fig. 1). The lingual and buccal extremities of the remaining laminae are rounded and not tapering as is generally the case in *P. namadicus* (Falconer & Cautley, 1845).

The occlusal surface of this deciduous molar is very worn, such that the crown is reduced to a height of only 19 mm. At the Geological and Palaeontological Museum of the University of Florence there are four Dp₃ (IGF 146, IGF 151, IGF 12791, IGF 12796) of *A. meridionalis* of the Upper Valdarno,



Text-fig. 1 - M_2 n. 272 (a, a') and Dp_3 n. 305 (b) occlusal surface (D. Migliorato drawings).

whose dimensions are similar to those of the deciduous molar from Steggio and are made of five-six laminae. In the same Museum there is a Dp_3 of *Palaeoloxodon antiquus* (Falconer & Cautley, 1845) (IGF 144) which is 72 mm long, 49 mm large and is made of six laminae. According to Maglio (1973), the Dp_3 of *A. meridionalis* are formed by 5-6 laminae and a lamellar frequency of 9.7-11.9.

The height of this premolar, and of other molars considered later in the text, has not been compared with that of other measured teeth of *A. meridionalis* because the latter do not belong to the same degree of wear or are in the alveolus.

Right M_1 (n. 110)

This complete molar is well preserved. It is composed of 9 laminae immersed in abundant cement and by three robust roots which are well separated. All the laminae have been used; the advanced wear on the anterior talon and on the first lamina resulted in their fusion. The enamel is quite folded.

Some of the biometric characteristics of the Steggio molar which are important for the identification of the species, coincide with those of the nine *A.*

meridionalis molars found at Pietrafitta and Upper Valdarno, and with the values which Garutt (1995) attributed to a find of the same species from Russia (Tab. 3).

In *Mammuthus trogontherii* Pohlig, 1885, the M_1 have 11-12 laminae and the enamel is 1.0-1.2 millimetres thick (Aguirre, 1969; Maglio, 1973).

Right M_2 (n. 272)

This right M_2 is complete and well preserved. The find is made up of 10 laminae plus the talons and it is characterised by abundant intralamellar cement. The enamel is only slightly folded. The last two laminae do not show any traces of use and the cusps of the eighth one have only just erupted. The third to the seventh laminae are arched, concave anteriorly (Text-fig. 1); the eighth one has six outcropping digitations; the highest lamina is the ninth one and none of them has a clear median sulcus.

The general dimensions, the number of laminae, the lamellar frequency and the LLQ all fall within the range of typical values for *Archidiskodon meridionalis* (Melentis, 1961; Aguirre, 1968; Maglio, 1973). The value of the "hypsodonty index-lamellar frequency"

Steggio		Valdarno			
		IGF 146	151	12791	12796
Length of the crown	47 (incomplete)	53	63	65	60
Width of the crown	40	38	38	38	34
Height of the crown	19	—	—	—	—
Number of laminae	- 4 x	x 5 x	x 5 x	x 6 x	x 6 x
Lamellar frequency	10	10	10	11	11
Enamel thickness	1.1 (0.9-1.2)	1 (0.9-1.2)	—	1.1 (1-1.2)	—

Tab. 2 - Dimensions of the Dp₃ from Steggio and four Dp₃ at the Geological and Palaeontological Museum of the University of Florence.

	Steggio	Russia (Garutt, 1995)	Pietrafitta	Valdarno
Length of the crown	152	151 (137-166)	153 (147-163)	156 (145-163)
Width of the crown	68	70 (64-87)	68 (65-74)	67
Height of the crown	77	—	—	—
Number of laminae	x 9 x	10 (9-11)	—	9 (8-10)
Lamellar frequency	6.7	6.3 (5.5-8)	6.5 (5-7.5)	6.7 (5.5-8)
LLQ	15	—	—	—
Enamel thickness	1.8 (1.6-2.1)	2.1 (1.5-2.8)	2.3 (1.5-3)	—

Tab. 3 - Main measurements of the M₁ from Steggio compared with the dimensions of some M₁ discovered in Russia, with the six molars found at Pietrafitta and with three molars all belonging to *A. meridionalis* found in the Upper Valdarno and stored at the Geological and Palaeontological Museum of the University of Florence (IGF 50, 126, 12794).

relationship falls within the range of the values attributed by Van Essen & Mol (1996) to the *A. meridionalis* molars found in the Netherlands. The low value of the angle of eruption of the molar (24°-25°) is also pertinent to *A. meridionalis* and excludes the possibility of it appertaining to the more advanced *M. trogontherii*. The value of this convex angle, which is comprised between the tangent plane of the occlusal surface and the plane which unites the lower extremities of the laminae, increases with the increase in height of the crown and is inversely proportional to the functional length (Aguirre, 1968). Meiring's hypsodonty index which was calculated for the Steggio molar is 68.7, while the value for this index calculated on six M₂ of *P. namadicus* discovered at Castel di Guido is comprised between 41.1 and 59.5. According to Dubrovo (1975), in the M₃ of *Palaeoloxodon* this index is always comprised between 46.6 and 60. The use wear on the laminae of molar n. 272 is similar to that on the molars from Valdarno.

With continued use, the molars change their characteristic morphology, and in particular the height, length, number of laminae and often the lamellar frequency as well. These variations can cause difficulties in the taxonomic identification, and perplexity in the phylogenetic reconstruction of the groups. Froehliche & Kalb (1995) have perfected a method which makes it possible to compare molars which have different degrees of wear. Adapting this method to the *A.*

meridionalis molars and applying it to that from Steggio, the latter falls within the WS-VII use wear stage (Text-fig. 1), which corresponds with the following description: the first, second and third lamina formed by a loop of closed and continuous enamel (3); the fourth, fifth and sixth lamina formed by two or three separated rings of enamel (2); the seventh lamina formed by more than three separate rings of enamel or which has some lamellar cusps which have not been worn (1); the eighth, ninth and tenth lamina not yet used (0).

Two M₂ of *A. meridionalis* (IGF 124, IGF 103), stored at the Geological and Palaeontological Museum of the University of Florence, have a very similar degree of use wear compared with that of the Steggio molar: these two molars have a lamellar frequency of 5.5, an average enamel thickness equal to 2.4 and a width of 75 and 84 mm, respectively. Some M₂ of *M. trogontherii* found in Croatia have 11-15 laminae and the enamel is 1.6-2.0 mm thick (Lenardic, 1991). Others M₂ of the same species found in the North Sea in the Netherlands have a lamellar frequency equal to 6.0-6.7 (Van Essen & Mol, 1996).

Rib (n. 224)

A fragment was found of the fourth or fifth rib which is lacking the articular surface and part of the ventral face. The bone is massive and has an elongat-

	Steggio	Valdarno	Pietrafitta
Length of the crown	225	206	227
Width of the crown	88	75-85	86 (80-95)
Height of the crown	127	100 (molar IGF 124)	103 (molar n. 388)
Number of laminae	x 10 x	x 10 x	9-11
Lamellar frequency	5	5,2 (5-6)	5.5 (4.5-6)
LLQ (I-VIII)	20	—	—
Enamel thickness	2.9 (2.8-3.1)	2.5 (2.2-3.1)	3 (2.4-3.9)

Tab. 4 - Measurements of the M_2 from Steggio compared with those of seven M_2 of *A. meridionalis* of which three are isolated teeth (IGF 68, IGF 103, IGF 124) and four are still fixed in the mandible (IGF 12, IGF 116) stored at the Geological and Palaeontological Museum of Florence University and thirteen M_2 from Pietrafitta.

ed tubercular crest. The maximum transversal diameter is equal to 90 mm and the axial length of the fragment is 69 mm.

Radius (n. 198)

The proximal articular surfaces are preserved as well as some fragments of the diaphysis of a right radius. The epiphysis has a well developed contact surface with the ulna. The maximum transversal diameter of the proximal epiphysis is 126 cm, while the diameters of the articulation face with the humerus are 116 x 75 mm.

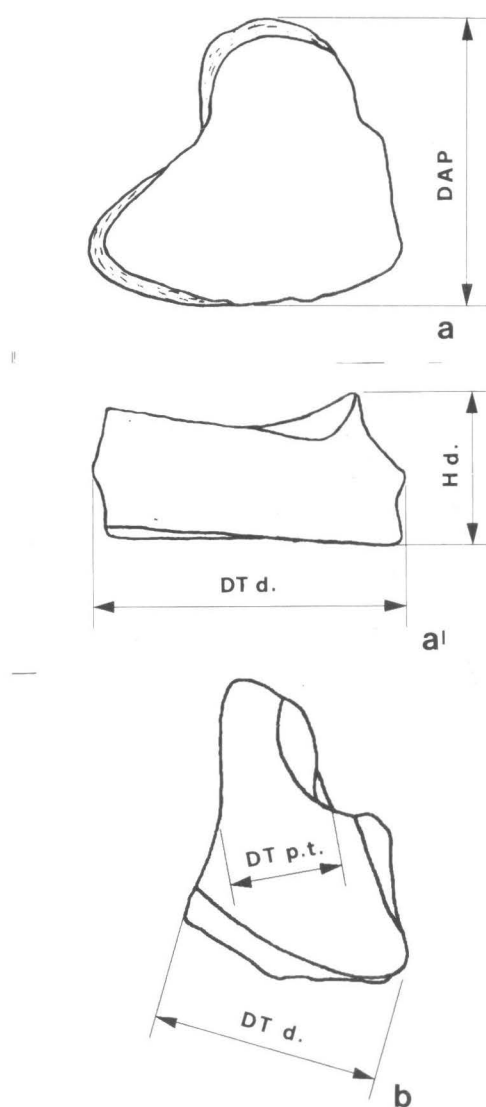
Carpals

One lunar (n. 180) is very well preserved while another one (n. 214) has been damaged although this has not altered the form of the bone. According to some authors (Vialli, 1956; Maccagno, 1962a; Dubrovo, 1985), these carpals have diagnostic characteristics if one considers the relationship with the carpals of the distal series, in particular with the magnum and the trapezoid.

The *A. meridionalis* lunars are proportionally shorter and taller than the *P. namadicus* and *P. antiquus* lunars. This difference is highlighted in Text-fig. 3, and in fact the values of the DAP/ dorsal DT- dorsal H relationship (Text-fig. 2) attributed to *A. meridionalis* can be separated from those attributed to other species, except for one find from Pietrafitta.

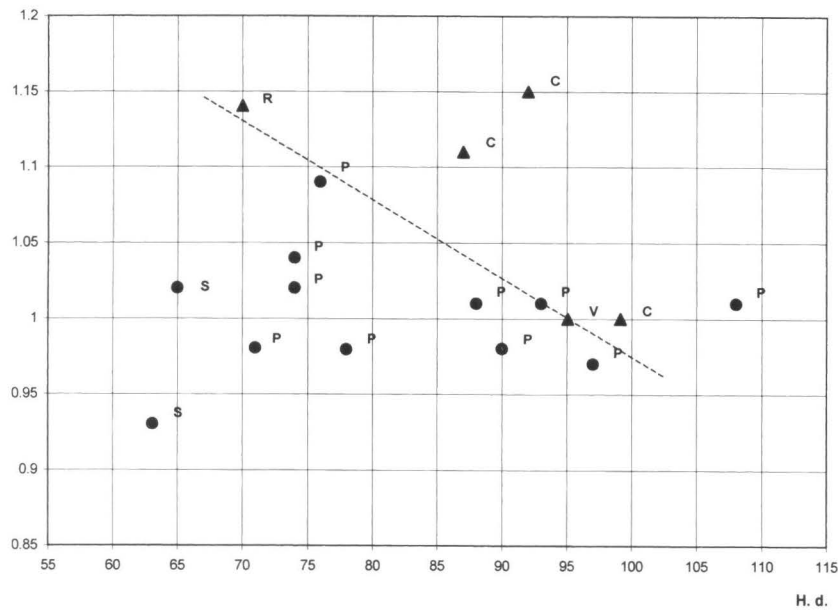
The two pyramidals n. 216 and n. 221 are badly preserved. N. 216 is broken into numerous pieces, while of n. 221 only the body has been preserved and the lateral apophysis is missing.

Two left trapezoids (n. 159/a and n. 207) were found, both of which lack a plantar fragment. The trapezoids of *A. meridionalis* have a smaller plantar tuberosity compared with those of *P. namadicus* (Text-fig. 4). This tuberosity, on which part of the facets of articulation with the scaphoid, magnum, trapezoid and second metacarpus develops, is short and narrow in *A. meridionalis* from Steggio and in *Archidiskodon* cf. *gromovi* from Savignano sul Panaro (Reggiani & Sala, 1994), and slightly wider in those



Text-fig. 2 - Lunar, a) viewed proximally, a') viewed dorsally. Trapezoid in proximal view (b). DAP = antero-posterior diameter; DT d. = transversal diameter of the dorsal face; Hd. = dorsal height; DT p.t. = transversal diameter of the plantar tuberosity.

DAP / DT d.



Text-fig. 3 - The relationship between the maximum dorsal height (H. d.) and the ratio DAP (antero-posterior diameter) / DT d. (dorsal breadth) in *A. meridionalis* (●), *P. namadicus* and *P. antiquus* (▲) from Steggio (S), Pietrafitta (P), Castel di Guido (C), Riano (R), Viterbo (V).

from Pietrafitta. To make this specific diversity more objective for comparisons, the percentage relationship was calculated between the transversal diameter of the plantar tuberosity, measured in correspondence with the notch present on the articulation facet with the magnum, and the transversal diameter of the dorsal face (Text-fig. 2). In the *A. meridionalis* specimens (two from Valdarno: IGF 14838, IGF 10791; and nine from Pietrafitta), this relationship varies between 34.5 and 46.5, while in the trapezoids of *P. namadicus* (Castel di Guido: n. 11733, n. 02282, n. 11783) and *P. antiquus* (Valdarno: IGF 1058) it is 57.3-60. In particular, in *A. meridionalis* from Steggio the value of this relationship is 45.9 and 34.5 in the trapezoids n. 159/a and n. 207, respectively. In the Steggio elephants the facet of articulation with the navicular has an accentuated torsion. In the *P. namadicus* trapezoids this facet has only a slight torsion and the edge of the axial side

forms an angle close to the median narrow part. The trapezoid of the elephant from Fonte Campanile, was described and illustrated by Trevisan (1948), also seems to have a form similar to that of the *P. namadicus* finds described here.

The left magnum n. 203 is complete and undeformed. The general form of this carpus is very variable in *A. meridionalis*. Viewed dorsally the find from Steggio is particularly narrow and tall; the areas of the surfaces of articulation with the second and third metacarpus are more or less the same.

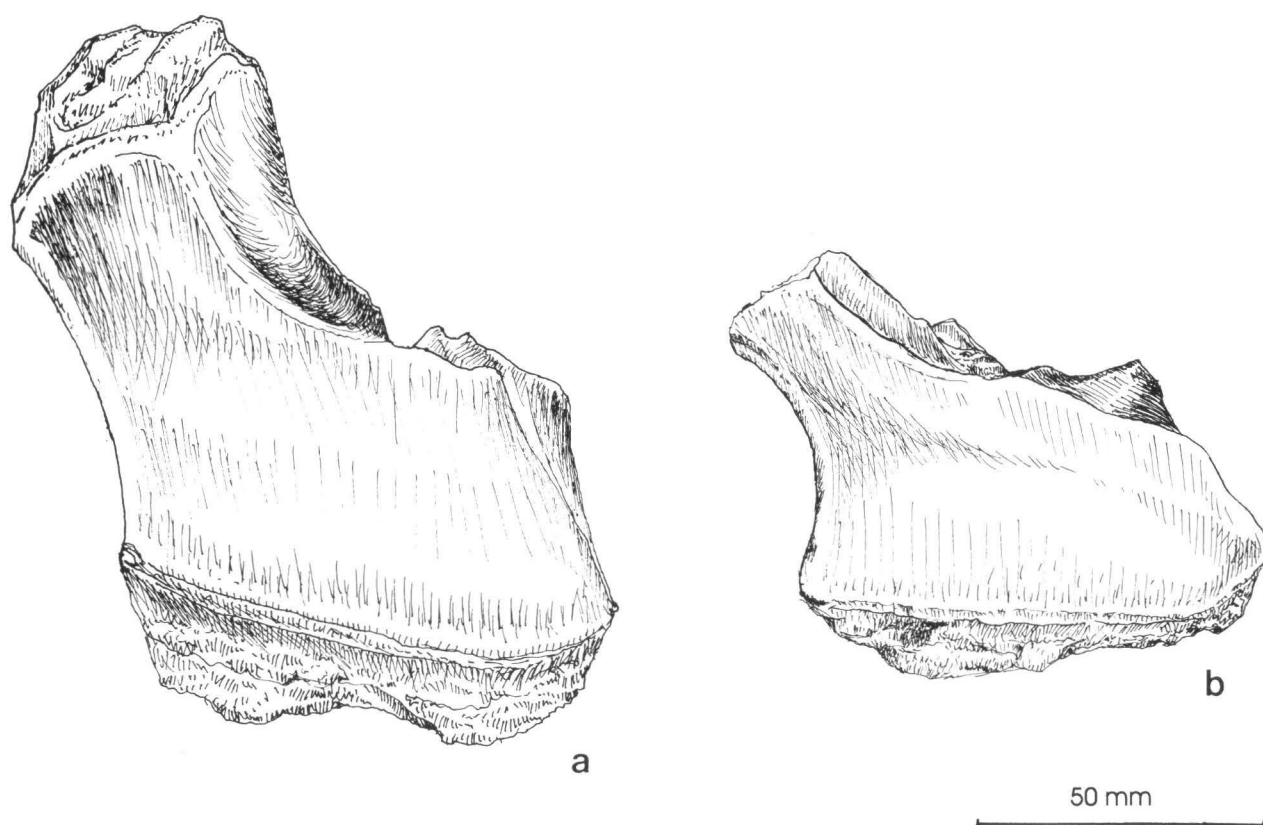
The unciform n. 159/b is in an excellent state of preservation but there are no important characteristics which can be used for species attribution.

Metacarpals

Three incomplete left metacarpals were found (II n.159/c, III n.181, IV n.314) which articulate per-

	Lunar		Pyramidal		Trapezoid		Magnum	Unciform
	n.180	n.214	n.221	n.216	n.159/a	n.207	n.203	n.159/b
DAP ma	114	132	117	125	—	—	137	94
DT max. dorsal face	122	130	—	—	74	84	—	—
H. max dorsal face	63	65	59	66	59	68	85	86
DAP art. ulna	—	—	98	107	—	—	—	—
DT art. ulna	—	—	109	—	—	—	—	—
DT dorsal art. lunar	—	—	—	—	—	—	82	—
DT dorsal art. III mc	—	—	—	—	—	—	52	—
DT lower dorsal face	—	—	—	—	—	—	—	106

Tab. 5 - Measurements of the *A. meridionalis* carpals from Steggio. Some of the abbreviations used: DAP = antero-posterior diameter; DT = transversal diameter; H = height; art. = articulation; max = maximum.



Text-fig. 4 - Left trapezoids in proximal view, a) *P. namadicus* n. 2282 from Castel di Guido, b) *A. meridionalis* n. 207 from Steggio (D. Migliorato drawings).

fectly together. Their small size suggests that they belong to the same animal which died at a young age. Of all three metacarpals only the proximal part was found.

The proximal epiphysis of the III metacarpus n. 181 was damaged during the excavation. The angle of the dihedron formed by the articulation facet for the magnum with that of the unciform (Pl. 1) is 105° at the apex in the find from Steggio, compared with 105° and 118° in the two III metacarpals from Pietrafitta. In the III metacarpus of *P. namadicus* n. 11737 from Castel di Guido this angle is 125° and about 132° in the *P. antiquus* from Riano, as can be calculated from the illustration published by Maccagno (1962b). In *A. cf. gromovi* from Savignano sul Panaro the angle is 100° (Reggiani & Sala, 1994). The facet of articulation with the magnum has a proportionately wider surface in *M. primigenius* with

respect to *A. meridionalis* (Felix, 1912; Chmielewski & Kubiak, 1962; Reggiani & Sala, 1992).

In the IV metacarpus n. 314 the facet of articulation for the V metacarpus extends along the whole of the peripheral edge. No significant characteristics were found in this bone which could be used for species attribution.

Hind limbs

At Steggio an elephant femur (n. 134) was found, as well as a fragment of a tibia, one calcaneum (n. 308) and one astragalus (n. 199).

The femur, which is small, is lacking the greater trochanter which had not yet fused with the diaphysis; its maximum length is 1120 mm and the transversal diameter of the diaphysis is 135 mm. In living elephants the proximal epiphyses of the femur fuse at an age of between 25 and 35 years (Haynes, 1991). In

	II metacarpus n. 159/c	III metacarpus n. 181	IV metacarpus n. 314
DAP proximal epiphysis	93	97	92
DT dorsal proximal epiphysis	80	—	82

Tab. 6 - Measurements of the metacarpals from Steggio

the find from Steggio the neck diverges from the axis by about 33 degrees, as is the case in the finds from Savignano sul Panaro and Lefte. The tibia is represented by a robust fragment of the diaphysis which has a minimum circumference of 350 mm.

The calcaneum and the astragalus are incomplete and badly preserved. The two finds are not well ossified and are of a small size, and consequently they have been interpreted as belonging to a juvenile individual.

The part of the astragalus occupied by the ectal articulation is well preserved. This articulation has a triangular shape and it measures 107x74 mm. The side of the ectal articulation which delimits the ligamentary fossa is rectilinear, like that of the female specimen from Savignano sul Panaro (Reggiani & Sala, 1994). In other individuals, such as *A. meridionalis* from Scoppito and *P. antiquus* from Riano, this side has a clear notch (Maccagno, 1962a, b).

DISCUSSION

The remains of *A. meridionalis vestinus* characterise the Farneta Faunal Unit which is generically attributed to the latest phase of the Late Villafranchian (Azzaroli, 1977; Azzaroli *et al.*, 1988; De Giuli, 1986; De Giuli *et al.*, 1983; Torre *et al.*, 1992), while *A. meridionalis meridionalis* is typical of the Olivola and Tasso Faunal Units which date to the beginning of the Late Villafranchian, circa 1.7-1.4 Ma (Azzaroli *et al.*, 1982, 1986; De Giuli & Masini, 1986; Torre *et al.*, 1992). According to Dubrovo (1985, 1990), in Russia it is possible to distinguish three different subspecies of *A. meridionalis*. Particularly interesting are the elephant remains discovered in the Taman peninsula from southern Russia; these elephants have been attributed to the evolved subspecies *A. meridionalis tamanensis* Dubrovo, 1977, which occurs in Lower Pleistocene deposits dated between 1.0 and 0.9 Ma. *A. meridionalis cromerensis* (Deperet & Mayet, 1923) represents the last stage of evolution of this group of European elephants, the remains of this subspecies are typical of English deposits dating back to Cromerian, about 0.7-0.6 Ma (Melentis, 1961; Azzaroli, 1977; Beden, 1986; Lister, 1996).

The finds from Steggio belong to at least three elephants which died at different ages. In fact one Dp₃ was found of an animal which died at a very young

age (probably between two and three years), one M² and one M₁ belongs to one or two young elephants, and one M₂ to an adult.

There are two M₂ stored at the Geological and Palaeontological Museum of the University of Florence which have been attributed to *A. meridionalis vestinus* (IGF 14888, IGF 1439V): these molars have a lamellar frequency of 6 and 6.5, respectively. I have not observed morphologies and lamellar frequency different from those typical of the molars of *A. meridionalis meridionalis* in the other two molars (IGF 14887, IGF 14838) attributed to this evolved subspecies.

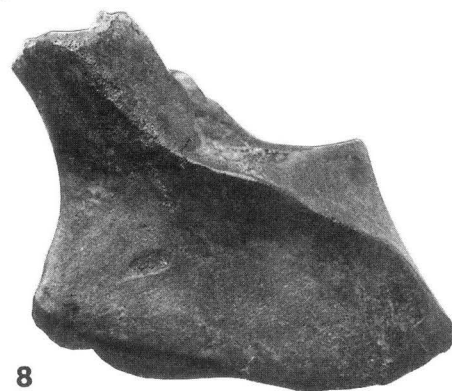
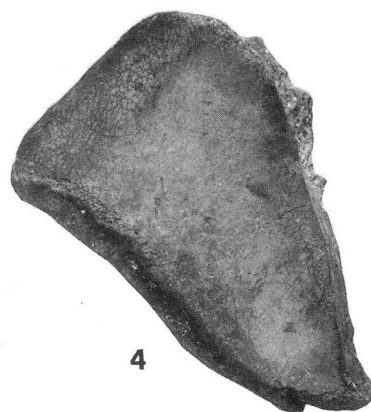
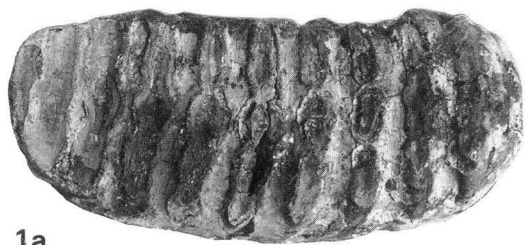
In *A. meridionalis tamanensis* the lamellar frequency is particularly variable (Dubrovo, 1985, 1990). The M₂ of the latter subspecies have a lamellar frequency comprised between 4 and 6.5 and a number of lamina which ranges from 10 to 13 (Azzaroli, 1977; Beden, 1986). Two fragments of M₂ of *Mammuthus meridionalis* cf. *tamanensis* from Oubeidiyeh (Beden, 1986) have a lamellar frequency equal to 5.7-5.6. At Tegelen (the Netherlands) various molars were found which appertain to a primitive form of *A. meridionalis*, and among these there is a M₂ (T5) which has an enamel thickness varying between 3 and 4 mm (Guenther, 1986). The M₂ of the specimens of *A. gromovi* from Chapry (Garutt & Bajguseva, 1981) have an average lamellar frequency of 4.1, while the M₁ are particularly narrow compared with those of *A. meridionalis*.

The molars from Steggio do not have the typical morphometric characteristics of the most primitive forms of *A. meridionalis* and *A. gromovi*. All the biometric values of the molars, which are important for the taxonomy of the Proboscidea, fall within the range of the measurements pertinent to *A. m. meridionalis* and do not reach the extreme values attributed to the more recent subspecies such as *A. m. tamanensis*, *A. m. cromerensis* and *A. m. vestinus*, but the M₁ and M₂ from Steggio have quite a high hypsodonty index. However, a sample made of only three molars is not sufficient to decide confidently whether these elephants were more or less developed, considering high intraspecific variability.

The carpal of the elephants is defined as "serial" when the lunar is placed only above the magnum, and the pyramidal is perfectly placed above the unciform. It is considered "aserial" when the lunar is even partially placed above the trapezoid and sometimes

EXPLANATION OF PLATE 1

Figs. 1-8 - *Archidiskodon meridionalis* (Nesti, 1825). Steggio (Possagno), Lower Pleistocene. Right M₁ n. 110 (1, 1a) and right M₂ n. 272 (2): 1) and 2) lingual surface, 1a) occlusal surface. M² n. 244/d in back view (3). Left radius n. 198 in viewed proximally (4). Left magnum n. 203 (5, 5a): 5) distal surface, 5a) proximal surface. Left lunar n. 214 in distal view (6). Left metacarpals II n. 159/c, III n. 181 and IV n. 314 in proximal view (7). Left trapezoid n. 207 in proximal view (8). Figures 1, 2, 3, 4, 5, 5a, 6, 7 are 37,5 % natural size, figure 1a is 45% and figure 8 is 74% natural size.



the unciform (Dubrovo & Mol, 1991; Aguirre, 1995; Lister, 1996). At Steggio no elephant carpals were found in anatomical connection, while a magnum (n. 203) and a lunar (n. 214) were found which articulate together and which have therefore been attributed to the same individual or to two individuals of similar dimensions. The articular relationship between these two carpals is decidedly aserial; in fact the lunar projects from the magnum by about 20% of its dorsal transversal diameter. This is in agreement with Vialli's (1956) description of the *A. meridionalis* from Leffe and with the carpals in anatomical connection housed in the Geological and Palaeontological Museum of the University of Florence (IGF 13094, IGF 14838). In the complete limbs of *M. trogontherii* found at Sangerhausen (Germania) the carpus and tarsus have an aserial structure (Dubrovo, 1975, 1985) while in *P. namadicus* the carpals seem to be serial (Trevisan, 1948) or slightly aserial (Maccagno, 1962b). Lister (1996) admits that in *A. meridionalis* the carpus structure may be serial or not fully serial. At Pietrafitta various anterior carpal bones were found in anatomical connection which have very variable relationships with the carpals of the first range and those of the second range. Some of the carpals have a decidedly aserial structure while others are serial.

Considering the notable diversity in the relationship between the carpal bones of *A. meridionalis*, it is likely that the articular relationship described is not an important characteristic for distinguishing between the most recent specimens of *A. meridionalis* and the more archaic ones, or for distinguishing between elephants of different species as Dubrovo (1975), Garutt (1998) and other authors claim.

The bones of the first and second range of the carpus of *A. meridionalis* are not only smaller but they are also generally narrower and taller than those of *P. namadicus* and *P. antiquus*; the carpus is therefore slimmer in the former, and stockier in the latter.

ACKNOWLEDGMENTS

I am particularly grateful to Professors A. Lister, G. Piccoli, B. Sala and M. Tonon for their critical reading of the manuscript and their precious advice. I would also like to thank Professors P. Ambrosetti, D. Torre and G. Billi for having allowed me to analyse the finds from Pietrafitta which are housed at the Museums in Florence and Montevarchi, and Doctors E. Cioppi, F. Cozzini and S. Gentili for helping me during the study of the Umbrian and Tuscan collections. Finally, I would like to thank D. Migliorato for the drawings, and Doctors L. Picin, C. Vaccari, G. Vitaliani and F. Reggiani for having contributed to the result of this work.

This work is supported by grants from C.N.R. (National Research Council of Italy) Committee 05 (97.04533).

BIBLIOGRAPHY

- AGUIRRE, E. E., 1968, Revision sistemática de los Elephantidae por su morfología y su morfometría dentaria (Primera parte): Estudios Geológicos, 24: 109-167.
- , 1969, Revision sistemática de los Elephantidae por su morfología y su morfometría dentaria (Segunda parte): Estudios Geológicos, 25: 123-177.
- , 1995, Proboscidea II - Los elefantes fósiles. In Melendez B., Paleontología 3 - Volumen 2. Editorial Paraninfo: 311-353, Madrid.
- AZZAROLI, A., 1949, Osservazioni sulla formazione villafranchiana di Olivola in Val di Magra: Società Toscana di Scienze Naturali, 56 (A): 104-111.
- , 1977, Evolutionary patterns of villafranchian elephants in central Italy: Accademia Nazionale dei Lincei, 14 (8): 149-170.
- , DE GIULI, C., FICCARIELLI, G. & TORRE, D., 1982, Table of the stratigraphic distribution of terrestrial mammalian faunas in Italy from the Pliocene to the early middle Pleistocene: Geogr. Fis. Dinamic. Quat., 5: 55-58.
- , —, & —, 1986, Mammal succession of Plio-Pleistocene of Italy: Memorie Società Geologica Italiana, 31: 213-218.
- , —, & —, 1988, Late Pliocene to Early Pleistocene mammals in Eurasia: faunal succession and dispersal events: Palaeogeography, Palaeoclimatology, Palaeoecology, 66: 77-100.
- BEDEN, M., 1986, Le mammouth d'Oubeidiyeh (Israel). In Tchervov E., Les mammifères du Pleistocène inférieur de la vallée du Jourdain a Oubeidiyeh: Mémoires et Travaux du Centre de Recherche Français de Jerusalem, 5: 213-234.
- CHMIELEWSKI, W. & KUBIAK, H., 1962, The find of Mammoth bones at Skararki in the Lowicz district: Folia Quaternaria, 249: 1 - 29.
- DE GIULI, C., 1986, Late Villafranchian faunas of Italy: the Selvella Local Fauna in the southern Chiana Valley - Umbria: Palaeontographia Italica, 74: 11-50.
- , FICCARIELLI, G., MAZZA, P. & TORRE, D., 1983, Confronto tra successioni marine e continentali del Pliocene e Pleistocene inferiore in Italia e nell'area mediterranea: Boll. Soc. Paleont. Ital., 22 (3): 323-328.
- & MASINI, F., 1986, Late Villafranchian faunas in Italy: the Casa Frata Local Fauna (Upper Valdarno, Tuscany): Palaeontographia Italica, 74: 1-9.
- DUBROVO, I. A., 1975, *Mammuthus trogontherii trogontherii* (Polig) aus dem Pleistozän von Tiraspol: Quartärpaläontologie, 1: 125-155.
- , 1985, Problems of the systematics of fossil elephants: Acta Zoologica Fennica, 170: 241-245.
- , 1990, The Pleistocene Elephants of Siberia. In Megafauna & Man, Discovery of America's Heartland: 1-8, Hot Springs, South Dakota.
- & MOL, D., 1991, Fossiele olifanten de Sovjet-Unie en Nederland: Cranium, 2: 77-87.
- FELIX, J., 1912, Das Mammuth von Borna. R. Voigtlanders Verlag, 52 pp., Leipzig.
- FORONOV, V. I., 1986, Elephants of the Genus *Archidiskodon* from the Late Pliocene and Pleistocene of the Kuznetsh Basin (southeastern West Siberia): Quartärpaläontologie, 6: 29-42.
- FROELICH, D. J. & KALB, J. E., 1995, Interrelationships of Late Neogene Elephantoids: new evidence from the Middle Awash Valley, Afar, Ethiopia: Geobios, 28(6): 727-736.
- GARUTT, W. E., 1995, The phanagorian elephant *Phanagoroloxodon mammonitoides* Garutt, 1957 from the Pliocene of the north-western Caucasus 2: Cranium, 12(2): 87-92.
- , 1998, Is there a genus *Archidiskodon* Pohlig, 1885, of the family Elephantidae Gray, 1821: Cranium, 15(1): 15-20.
- & BAJGUSEVA, V. S., 1981, *Archidiskodon gromovi* Garutt & Alexeeva - der älteste Elefant der Mammuthlinie in Eurasia: Quartärpaläontologie, 4: 7-18.

- GENTILI, S., ABBAZZI, L., MASINI, F., AMBROSETTI, P., ARGENTI, P. & TORRE D., 1996, Vales from the Early Pleistocene of Pietrafitta (central Italy, Perugia): *Acta Zool. Cracov.*, 39 (1): 185-199.
- GHIOTTO, P., 1995, Contributo preliminare allo studio della macroflora del bacino lacustre «Villafranchiano» di Steggio (Prealpi venete, Italia settentrionale): *Il Quaternario*, 8 (1): 193-202.
- GUENTHER, E. W., 1986, Funde von *Archidiskodon meridionalis* und von *Trogontherium cuvieri* aus den interglazialen Tegelen-Schichten: *Quartärpaläontologie*, 6: 53-65.
- HAYNES, G., 1991, Mammoths, mastodonts, and elephants – Biology, behavior, and the fossil record. Cambridge University Press, 413 pp., Cambridge.
- LENARDIC, J., 1991, Kranijalni dijelovi, mandibule i izolirani zubi Pleistocenskih Slonova Raznih lokaliteta hrvatske i Vojvodine: *Geoloski Vjesnik*, 44: 15-29.
- LISTER, A. M., 1996, Evolution and taxonomy of Eurasian mammoths. In Shoshani J. & Tassy P. (eds.), *The Proboscidea*, Oxford University Press: 203-213, Oxford.
- MACCAGNO, A. M., 1962a, L'*Elephas meridionalis* Nesti di contrada «Madonna della strada», Scoppito (L'Aquila). Istituto di Geologia e Paleontologia Univ. di Roma, 132 pp.
- , 1962b, Gli elefanti fossili di Riano (Roma): *Geologica Romana*, 1: 33-131.
- MAGLIO, M., 1973, Origin and evolution of the Elephantidae: *Transaction of the American Philosophical Society*, N. S., 63(3): 149 pp., Philadelphia.
- MELENTIS, J. K., 1961, Die dentition der pleistozane Proboscider des Beckens von Megalopolis im Peloponnes (Griechenland): *Annales géologiques des Pays Helléniques*, 12: 153-262.
- OSBORN, H. F., 1942, Proboscidea: *American Museum Nat. Hist.*, 2: 805-1675, New York.
- PARONUZZI, P., 1993, Processi torbidity nella successione lacustre villafranchiana del bacino intermontano di Steggio (Treviso): *Atti Convegno AIQUA*, Roma 1993, *Il Quaternario*, 6: 358-361.
- & TONON, M., 1992, Il bacino lacustre villafranchiano di Steggio (Prealpi venete, Treviso) : primi dati stratigrafici ed evidenze neotettoniche: *Il Quaternario*, 5: 251-268.
- REGGIANI, P. & SALA, B., 1992, I Mammut del Veneto: *Memorie di Scienze Geologiche*, 44: 171-191.
- & —, 1994, *Archidiskodon* cf. *gromovi* (Proboscidea, Elephantidae) from Savignano sul Panaro, Modena (Northeastern Italy): *Memorie di Scienze Geologiche*, 46: 313-327.
- SALA, B. & BARBI, G., 1996, Descrizione della fauna. In Gli scavi a Castel di Guido, il più antico giacimento di cacciatori del Paleolitico inferiore nell'Agro Romano. Istituto Italiano di Preistoria e Protostoria: 55-90, Firenze.
- & TONON, M., 1992, *Eucladoceros* cf. *senezensis* Deperet 1910 in un bacino lacustre Villafranchiano a Steggio (Possagno, Treviso, Italia Nord-Orientale): *Il Quaternario*, 5: 11-16.
- TONON, M., 1994, Steggio una storia di argilla e di fossili. Media House Editore, 160 pp., Cosenza.
- TORRE, D., FICCARELLI G., MASINI, F., ROOK, L. & SALA, B., 1992, Mammal dispersal events in the Early Pleistocene of Western Europe: *Courier Forsch.-Inst. Senckenberg*, 153: 51-58.
- TREVISAN, L., 1948, Lo scheletro di *Elephas antiquus italicus* di Fonte Campanile (Viterbo): *Palaeontographia Italica*, 44: 1-78.
- VAN ESSEN, H. & MOL, D., 1996, Plio-Pleistocene proboscideans from the southern bight of the North Sea and the Eastern Scheldt, The Netherlands. In Shoshani J. & Tassy P. (eds.), *The Proboscidea*, Oxford University Press: 214-224, Oxford.
- VIALI, V., 1956, Sul rinoceronte e l'elefante dei livelli superiori della serie lacustre di Leffe (Bergamo): *Mem. Soc. Ital. Sci. Nat. Mus. Civ. St. Nat. Milano*, 12: 1-70.

(manuscript received May 14, 1998
accepted January 20, 1999)

Paolo REGGIANI

Via Zabarella 21
35028 Piove di Sacco (PD), Italy