

Mammuthus cf. *primigenius* (Proboscidea, Mammalia), a new faunal element from the late middle Pleistocene of the Conca river (Cattolica, Romagna, Italy)

Marco P. FERRETTI

Dipartimento di Scienze della Terra
Università di Firenze

KEY WORDS – Mammalia, *Mammuthus primigenius*, Systematics, Late Middle Pleistocene, Italy.

ABSTRACT – Remains of a mammoth from the late middle Pleistocene fluvio-lacustrine deposits outcropping along the flow of the Conca river (Cattolica, Romagna, Italy), are described. The material is referred to *M. cf. primigenius*, which represents a new element of the Conca fossil mammal fauna, attributed by Conti et al. (1982) to the penultimate cold stage. The morphometric characters of the Conca mammoth do not exclude the possibility it belongs to a more primitive form than typical late Pleistocene *M. primigenius*.

RIASSUNTO – [*Mammuthus* cf. *primigenius* (Proboscidea, Mammalia) nuovo elemento dal tardo Pleistocene medio del Torrente Conca (Cattolica, Romagna, Italia)] – Vengono descritti i resti di un mammut rinvenuti nei depositi fluvio-lacustri pleistocenici affioranti lungo il corso del Torrente Conca (Cattolica). Il materiale è attribuito a *M. cf. primigenius*, nuovo elemento della fauna fossile a mammiferi del Torrente Conca, riferita al penultimo Glaciale (Conti et al., 1982). I caratteri morfometrici del mammut del Conca non escludono la possibilità che l'esemplare appartenga ad una forma più primitiva di *M. primigenius* del Pleistocene superiore.

INTRODUCTION

The fluvio-lacustrine deposits that outcrop along the middle course of the Conca river (Cattolica, Romagna, Italy) yielded several mammal species in association with palaeolithic artefacts (Conti *et al.*, 1982).

The sediments rest on small depressions of the Pliocene marine bedrock and are topped by an erosive surface at the base of a pebbly fluvial sequence making up a 3rd order terrace of the northern Marche terrace-alluvium sequence (Nesci & Savelli, 1991).

The fluvio-lacustrine sequence was attributed by Conti et al. (1982) to the penultimate Glacial on pedo-stratigraphic, archaeological and faunistic evidence. In particular, the occurrence among the micromammals, that include also *Clethrionomys glareolus* and *Microtus* ex gr. *arvalis-agrestis*, of *Arvicola* cf. *terrestris* with almost undifferentiated enamel and *Castor fiber* with a primitive dental morphology was interpreted by Sala (in Conti *et al.*, 1982) as evidence of a pre-“Würmian” age. The large mammals, represented by *Ursus arctos*, *Stephanorhinus* cf. *hemitoechus*, a small sized *Equus*, *Bison priscus*, medium to small sized cervids and a megalocetine tentatively referred to *Megaloceros giganteus*, likewise compare with faunas from stadials of the penultimate cold stage from western Europe (Conti *et al.*, 1982; Sala *et al.*, 1992), even though all the taxa mentioned persisted well into the last cold stage.

On the other hand, Nesci and Savelli (1991) attributed the deposits to the last Glacial, on the grounds of unpublished radiometric datings of wood remains successively retrieved from the same outcroppings (Forlani, 1987).

Thus, even though the results of the multidisciplinary study by Conti *et al.* (1982) strongly support an attribution of the Conca mammal association to the penultimate Glacial, the possibility that part of the fauna is younger cannot be ruled out.

Prior to the discovery of the mammoth remains described in this paper, elephantids were documented in the Conca fluvio-lacustrine sequence only by a tusk fragment (Conti *et al.*, 1982).

SYSTEMATICS

Family ELEPHANTIDAE Gray, 1821
Subfamily ELEPHANTINAE Gray, 1821
Genus MAMMUTHUS Brooks, 1826

MAMMUTHUS cf. PRIMIGENIUS Blumenbach, 1799
Pl. 1, figs. 1-6

Material – Right upper M² (Pl. 1, figs. 1-2); fourth dorsal vertebra (Pl. 1, fig. 3); corpus of first or second lumbar vertebra (Pl. 1, fig. 4); incomplete rib (Pl. 1, fig. 5); fragmented left humerus (Pl. 1, fig. 6); several unidentified skeletal fragments. The material

is housed in the "Museo del Territorio di Riccione" (Rimini), with the rest of the Conca fauna.

Description and comparison – The remains, all badly preserved, probably belong to the same individual. This is suggested by their size and the absence of more than one skeletal element from each part of the body.

Moreover, the presence of an M^2 in function is consistent with the state of skeletal fusion of the dorsal vertebra and of the distal epiphysis of the humerus (see Sikes, 1967 and Roth, 1984).

Comparisons were made with specimens representative of various species of the genus *Mammuthus* known from the Plio-Pleistocene of Europe. Samples directly studied include the early Pleistocene (Late Villafranchian) *M. meridionalis* from Upper Valdarno (Tasso F.U.) and Pietrafitta, near Perugia (Farneta F.U.); *Mammuthus "primigenius"* (material in revision) from Ponte alla Nave and Maspino (Arezzo basin), referable to the late middle Pleistocene (De Giuli, 1983); the type population of *M. trogontherii* from the early middle Pleistocene of Süssenborn, Germany; the mammoth specimen from Via Flaminia Km 8.2 near Rome (Palombo, 1972), referred to *M. chosaricus* (= *M. trogontherii chosaricus*, Dubrovo, 1966) by Kotsakis *et al.* (1978) and dated to the late middle Pleistocene. The data on the *M. primigenius* population from the late Pleistocene of Predmostí (Czech Republic) used for the bivariate analysis are those reported by Musil (1968).

Finally, to extend the comparisons of the skeletal elements, focusing on their size, post-cranial elements of extant *Elephas maximus*, of middle Pleistocene *E. antiquus* from various Italian localities (see appendix), and of the small sized *E. mnaidriensis* from the late Pleistocene of Sicily, have been considered.

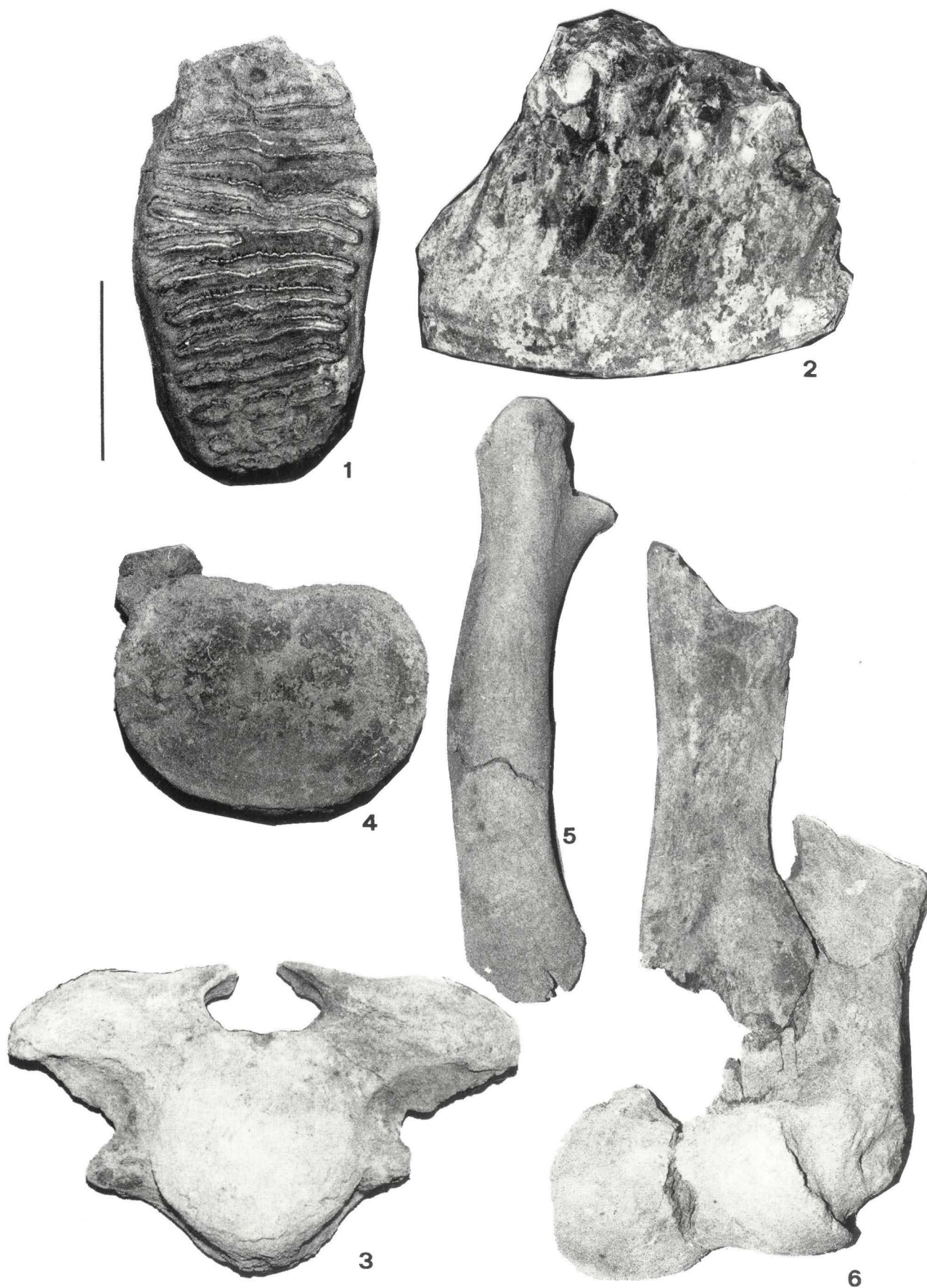
Dentition. Only an isolated molar is present. The longitudinally convex and relatively broad occlusal surface indicate that the tooth is an upper one. The greatest breadth of the crown and the morphology of its distal side agree with a M^2 . The molar bears 13 plates, all in use and a distal talon still unworn. At this stage of wear the crown height have been greatly reduced and the most mesial plates could have been

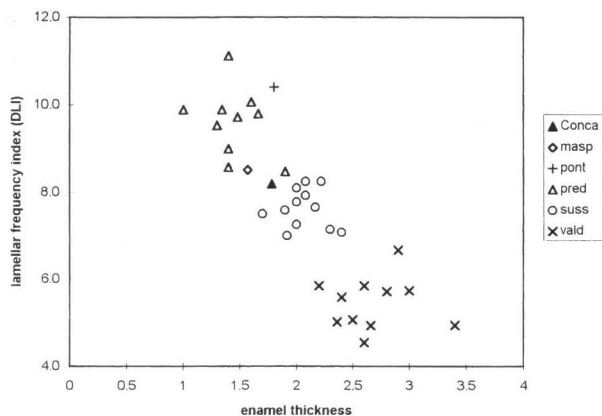
already shed, diminishing thus the original length of the crown and the plate formula. Nevertheless the dimensions of the occlusal surface can be still considered maximal. In particular functional length (FL) begins to reduce only after the wear plane has reached the distal talon, as plates are lost mesially. The Conca molar is characterised by a relatively broad wear surface and its occlusal length / occlusal breadth ratio is close to the mean values found for both *M. trogontherii* and *M. primigenius* (see appendix). The morphology of the enamel loops on the occlusal surface, recalls that of *M. primigenius* and is characterised by slightly folded enamel. Anterior to the most mesial plate an extended dentine area suggests the presence of one more plate now almost completely worn. Since the wear of the tooth at the front seems to have gone just beyond the level of the anterior root complex, it is likely that the dentine field represents the third or fourth plate. Thus a plate formula of 16-17 can be inferred for the unworn tooth. The first value corresponds with the maximum number of plates in the upper second molars of *M. trogontherii* from Süssenborn and with the minimum found for *M. primigenius*. Between the 6th and 7th plate, labial to the medial axis of the tooth, there is a partial plate provided with an independent root (Pl. 1, fig. 1). Its presence likely caused, during the development of the tooth, the visible forward displacement of the labial half of the lamellae anterior to it. This anomaly has no consequence on occlusion and it seems, from personal observations, to occur more frequently in molars of *M. primigenius* than in those of other species. The lamellar frequency index (DLI = number of plates / crown mesiodistal length) and the functional lamellar frequency index (Q = plates in function / occlusal length) of the Conca M^2 , have been computed as the mean between the values obtained separately for the lingual and the labial side, where also the semi-plate has been counted. The two indexes furnished values which fall near the maximum found for *M. trogontherii*, but are not as high as those that characterise most of the *M. primigenius* molars (Text-fig. 1). The enamel thickness is near the lowermost values found for *M. trogontherii*.

The bivariate analysis (Text-fig. 1) demonstrates also that the two M^2 from Ponte alla Nave and Maspino are biometrically very close to that from

EXPLANATION OF PLATE 1

- Figs. 1-6 - *Mammuthus* cf. *primigenius* from Conca River.
 1,2) Right upper M^2 , occlusal view (1) and labial view (2).
 3) 4th dorsal vertebra, cranial view.
 4) 1st or 2nd lumbar vertebra, caudal view.
 5) Rib, proximal portion.
 6) Left humerus, distal portion.
 The scale is about 5 cm for Figs. 1-5, 10 cm for Fig. 6.

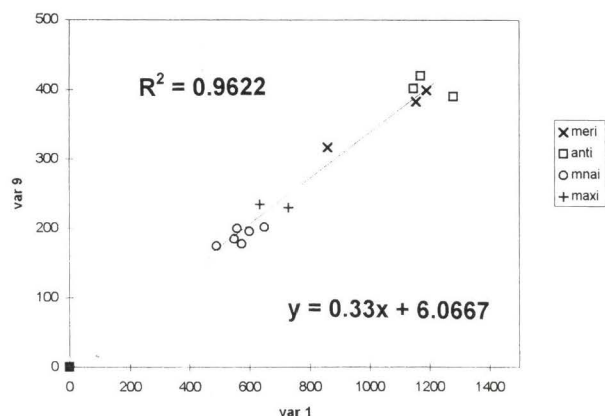




Text-fig. 1 - Scatter diagram of upper M^2 enamel thickness versus lamellar frequency index for some species of *Mammuthus*. Conca = *Mammuthus* from Conca river; masp = *Mammuthus* from Maspino; pont = *Mammuthus* from Ponte alla Nave; pred = *M. primigenius* from Predmostí (data from Musil, 1968); suss = *M. trogontherii* from Süssenborn; vald = *M. meridionalis* from Upper Valdarno.

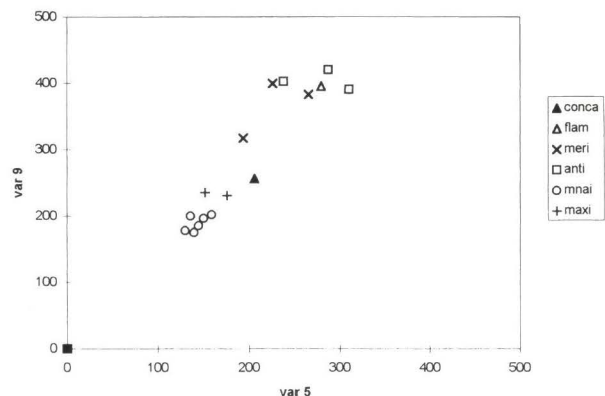
Predmostí and their morphology further supports this similarity.

Post-cranial elements. The dorsal vertebra lacks the neural spine. The vertebral arch, the cranial and the caudal articular surfaces are fully fused with the corpus (Pl. 1, fig. 3). Of the lumbar vertebra, possibly the first or the second one, only the corpus is represented, with the two articular heads already fused (Pl. 1, fig. 4). The incomplete humerus consists of the distal end and part of the shaft. The distal epiphysis is fused to the diaphysis (Pl. 1, fig. 6). In the appendix an estimate of the original length of the humerus is reported. This values has been obtained from the regression equation showed in Text-fig. 2, on the basis of the length of the epicondylar crest (EP-L) and the greatest length (GL) of the humeri used for comparison conformed to a linear regression model. The dimensions of the few preserved skeletal remains of the Conca mammoth, if compared with those of other elephant species, reveal a medium sized individual, close to *E. maximus* (Text-fig. 3 and appendix) and *M. primigenius* (cf. Kulczycki, 1955). Small size is a characteristic of late *Mammuthus* forms and, as can be seen from Text-fig. 3, differentiates the Conca specimen from both *M. meridionalis* and the Via Flaminia (Rome) mammoth. However, these features could represent only an individual character possibly related to sex (in extant elephant females are usually much smaller than males of the same age). It is here interesting to note that despite its modest size the Conca mammoth is characterised by relatively large teeth.



Text-fig. 2 - Scatter diagram of humerus greatest length (VAR 1) versus length of the epicondylar crest (VAR 9) for some elephant species, showing regression line and equation and coefficient of determination. The regression equation was used to estimate the greatest length of the Conca mammoth humerus; meri = *M. meridionalis* from Upper Valdarno and Pietrafitta; anti = *Elephas antiquus* from various sites; mnai = *E. mnaidriensis* from Sicily; maxi = *E. maximus*, captive.

The M^2 is actually the only element which allows some taxonomic assessment about the Conca river mammoth. Most of the metrical characters of the tooth fall within the overlap zone between the *M. trogontherii* and *M. primigenius* ranges, while the features of the occlusal surface are closer to those of the latter species. Unfortunately, no data on M^2 of any of the regarded intermediate forms between *M. trogontherii* and *M. primigenius* reported in the literature, as *M. t. chosaricus* (Dubrovo, 1966, 1992; Lister,



Text-fig. 3 - Scatter diagram of humerus distal articular width (VAR 5) versus length of the epicondylar crest (VAR 9) for some elephant species. Conca = *Mammuthus* from Conca river; flam = *M. chosaricus* (= *M. trogontherii chosaricus*) from via Flaminia Km. 8.2 (Rome); other abbreviations as in Text-fig. 2.

1996), were available for a direct comparison. For these reasons a definite attribution of the Conca mammoth cannot be given, at least until more material is found.

However, giving a greater weight to the derived characters presented by its molar (occlusal morphology, relatively high DLI and thin enamel) the Conca river mammoth is tentatively referred to *M. cf. primigenius*.

CONCLUDING REMARKS

The occurrence of a mammoth closely related to *M. primigenius* in the late middle Pleistocene deposits of the Conca river suggests a cold-open biotope, as already concluded by Sala (in Conti *et al.*, 1982) on the basis of the presence of *Microtus ex gr. arvalis-agrestis* and other open habitat dwellers as *Bison priscus* and the horse. On the other hand, the occurrence of *Castor fiber*, *Arvicola terrestris*, *Clethrionomys glareolus*, *Ursus arctos* and the medium to small cervids in the association, also suggests that such cold grassland gave place laterally to forested areas. It cannot be excluded, however, that, at least, some of these latter taxa pertain, actually, to a different level, possibly representing an interstadial.

It is a commonly shared opinion that *M. primigenius*, widespread through the northern hemisphere during the last Glacial, differentiated from the early middle Pleistocene *M. trogontherii*. Still not completely clarified, however, is the systematic position of the penultimate Glacial mammoths. Several samples from late middle Pleistocene European localities have been regarded as forms morphologically intermediate between *M. trogontherii* and *M. primigenius*. These include, among the others, *M. primigenius fraasi* from Steinheim (Dietrich, 1912) and *M. trogontherii chosaricus* (*M. chosaricus* according to some Authors) from Cernji Ar in the Volga Valley (Dubrovo, 1966).

Broadly referable to the same interval of the middle Pleistocene are also some specimens, like those from Bucine (Upper Valdarno, 3rd lacustrine phase), the Arezzo basin (Ricci, 1901; De Giuli, 1983) in Italy and Balderton in England (Lister & Brandon, 1991), that possess instead derived dental characters and are virtually indistinguishable from *M. primigenius*. At present it cannot be excluded that these late middle Pleistocene forms represent, indeed, a highly polymorphic species, as suggested by several Authors (Aguirre, 1968-69; Kahlke, 1994). Moreover, Lister & Joysey (1992) showed that differences between mammoth samples in two important evolutionary dental parameters, such as lamellar frequency and enamel thickness, may be sometimes merely an effect of tooth size variations.

As for the Conca mammoth, the particular morphological and metrical characters of its M^2 make it equally possible it belongs to a *M. primigenius* population or to a less derived form ("*fraasi-chosaricus*" group) and therefore it is not informative about the actual age (whether penultimate or last Glacial) of the Conca fluvio-lacustrine deposits.

ACKNOWLEDGEMENTS

I am grateful to all the persons that let me study materials in their charge. In particular, I would like to thank the Director of the "Museo del Territorio" of Riccione and the "Soprintendenza Archeologica" of the Emilia Romagna region for allowing me to study the Conca mammoth material. I am indebt with Dr. C. Giovagnetti and Dr. M. Sami for their help and to Dr. A. M. Lister for his useful discussion. I am grateful to Prof. G. Ficarelli, Dr. L. Rook and Prof. D. Torre for their suggestions and critical reading of the manuscript and to Prof. F. Masini and Prof. B. Sala for their comments. The photographs have been printed by Mr. F. Landucci. The mammoth remains were found by Mr. G. Conti who collected also all the previous material from the Conca river deposits. Work supported by M.U.R.S.T. grants.

APPENDIX - Material

Abbreviations : (museum and institutes)- ACM: Museo di Anatomia Comparata, Bologna; IGF: Museo di Geologia e Paleontologia, Florence; IQW: Institut für Geowissenschaften Bereich Quartärpaläontologie, Weimar; MPR: Museo di Paleontologia, Roma; MSNM: Museo Civico di Storia Naturale, Milano; MTR: Museo del Territorio di Riccione; MZLP: Museo di Zoologia La Specola, Firenze; NCM: Museo Paleontologico Valdarnese, Montevarchi (nuovo catalogo); PA: Centrale Termoelettrica Enel, Pietrafitta; (dental measures)- ET: enamel thickness; FB: occlusal (functional) breadth; FL: occlusal (functional) length; GB: greatest bucco-lingual breadth; GH: greatest height; GL: greatest mesio-distal length; PF: plate formula; U: number of plates in use; (humerus measures) VAR1: greatest length; VAR2: length from humeral head; VAR3: minimal transverse diameter at mid-shaft; VAR4: minimal antero-posterior diameter at mid-shaft; VAR5: distal articular width; VAR6: width of coronoid fossa; VAR7: transverse diameter of humeral head; VAR8: antero-posterior diameter of humeral head; VAR9: length of epicondylar crest; (vertebrae measures)- VAR1: transverse diameter of centrum (anteriorly); VAR2: transverse diameter of centrum (posteriorly); VAR3: height of centrum (anteriorly); VAR4: height of centrum (posteriorly); VAR5: dorsal antero-posterior diameter of centrum; VAR6: median a.-p. diam. of centrum; VAR7: ventral a.p. diam. of centrum; VAR8: greatest transverse diameter; VAR9: greatest transverse diameter of neural foramen.

M.cf. primigenius from Conca River - M/2 measurements

Specimen	GL	FL	GB	FB	GH	PF	U	ET
MTR	>173	161	92	81	>109	>14,5	13,5	1,8

M. primigenius from Maspino and Ponte alla Nave (Arezzo) - M/2 measurements

Specimen	GL	FL	GB	FB	GH	PF	U	ET
IGF 1086	195	104	77	59	141	18	10	1,6
IGF 5225	164	159	69	61	-	17	14	1,8

M. trogontherii from Süssenborn - M/2 measurements

Specimen	GL	FL	GB	FB	GH	PF	U	ET
IQW 65/2928	200	123	90	70	168	15	10	1,7
IQW 69/1193	170	157	90	78	150	14	13	2,0
IQW 66/6924	198	186	92	-	138	14	14	2,4
IQW 66/7080	206	-	83	-	152	16	5	2,0
IQW 65/2468	198	-	79	-	153	16	7	-
IQW 65/2862	173	-	75	-	158	14	6	2,0
IQW 65/2909	182	-	68	59	147	15	8	2,0
IQW 65/3233	210	139	92	77	176	15	11	2,3
IQW 65/2449	170	140	90	74	159	13	11	2,0
IQW 65/3125	202	-	82	66	164	16	8	2,1
IQW 65/2478	200	-	77	62	169	14	6	2,1
IQW 65/2346	193	150	90	73	160	15	12	1,9

M. meridionalis from Upper Valdarno - M/2 measurements

Specimen	GL	FL	GB	FB	GH	PF	U	ET
NCM 38/18	219	119	-	76	119	11	6	2,4
NCM 40/8	205	135	84	73	104	12	8	2,6
NCM 37/16	205	143	96	87	105	12	9	2,2
IGF 43	197	78	86	69	110	11	4	2,4
IGF 78	217	103	83	-	123	11	5	2,5
IGF 12790	192	192	83	83	77	11	11	3,0
VFT 214	175	-	90	-	103	10	-	2,8
VFT 347	223	144	103	82	140	11	7	2,7
VFT 203	180	143	70	-	-	12	9	2,9
IGF 21	243	156	92	88	148	12	8	3,4
IGF 20	220	125	102	81	-	10	6	2,6

M. primigenius from Predmosti - M/2 measurements (from Musil, 1968)

Specimen	GL	FL	GB	FB	GH	PF	U	ET
PR 20603	153	125	-	72	144	17	13	1,4
PR 21866	184	57	-	51	147	18	5	1,6
PR 21877	189	186	-	76	117	16	16	1,9
PR 22026	175	140	-	75	130	17	12	1,4
PR 22016	162	130	-	67	135	16	13	1,0
PR 21981	169	110	-	62	130	16	10	1,4
PR 21977	189	127	-	-	148	18	11	1,3
PR 22195	190	36	-	63	143	18	3	-
PR 21975	178	83	-	53	136	16	8	1,4
PR 21887	173	60	47	-	128	17	6	1,6
PR 9013	187	172	84	-	130	16	16	1,4

Humerus measurements											
Species	Locality	Specimen	VAR1	VAR2	VAR3	VAR4	VAR5	VAR6	VAR7	VAR8	VAR9
<i>M. meridionalis</i>	Upper Valdarno	IGF 318	1190	-	153	162	226	121	224	242	399
<i>M. meridionalis</i>	Upper Valdarno	IGF 320	859	897	100	122	194	86	135	187	317
<i>M. meridionalis</i>	Pietrafitta	PA-D	1155	1180	148	-	272	107	215	263	390
<i>M. meridionalis</i>	Pietrafitta	PA 66	1220	-	-	-	-	-	-	-	-
<i>E. mnaidriensis</i>	Sicily	IGP 24626	560	580	83	80	136	66	-	150	200
<i>E. mnaidriensis</i>	Sicily	IGP 24627	575	600	73	82	130	57	120	136	178
<i>E. mnaidriensis</i>	Sicily	MSNM V	490	580	77	74	140	-	118	139	175
<i>E. mnaidriensis</i>	Sicily	MSNM V 2873	600	610	79	73	150	60	125	142	196
<i>E. mnaidriensis</i>	Sicily	MSNM V 2874	570	575	70	60	145	55	138	115	185
<i>E. mnaidriensis</i>	Sicily	MSNM V 2871	650	660	83	70	159	65	-	152	202
<i>E. maximus</i>	Asia	MZLP 734	730	760	70	95	176	72	122	155	230
<i>E. maximus</i>	Zoo	ACM 4901	635	626	57	61	152	62	117	134	235
<i>E. antiquus</i>	Upper Valdarno	IGF 1058	1170	1170	155	105	230	90	210	265	400
<i>E. antiquus</i>	Monte Sacro	MPR	1280	1212	150	163	310	96	-	280	390
<i>E. antiquus</i>	Grotte S. Stefano (Viterbo)	MPR	1170	1200	150	195	287	97	192	320	420
<i>M. cf. primigenius</i>	Torrente Conca	MTR	759 *	-	-	-	206	-	-	-	256
<i>M. chosaricus</i>	Via Flaminia Km 8.2	MPR	-	-	168	132	279	108	-	-	395

* reconstructed

M. cf. primigenius from Conca River - vertebrae measurements

Specimen	VAR1	VAR2	VAR3	VAR4	VAR5	VAR6	VAR7	VAR8	VAR9
4th dorsal vert.	121	142	124	134	66	72	70	290	66
1st or 2nd lumbar vert.	150	-	117	-	-	-	76	-	-

REFERENCES

- AGUIRRE, E., 1968-69, Revision sistemática de los Elephantidae por su morfología y biometría dentaria: Est. Geol., 24 (3-4): 109-167; 25 (1-4): 123-177, 317-367, Madrid.
- CONTI, G., CREMASCHI, M., PERETTO, C., SALA, B., & UNGARO, S., 1982, Deposito fluvio-lacustre pre-wurmiano con faune e industrie del torrente Conca (Riccione, Forlì). Atti XXIII Riun. Sc. Ist. It. Preist. Protost. (Firenze 7-9 maggio, 1980): 307-328.
- DE GIULI, C., 1983, Aspetti paleontologici delle successioni del Valdarno Superiore e del Bacino di Arezzo. In I depositi fluvio-lacustri del Valdarno Superiore. Guida alla escursione del Gruppo Informale "Sedimentologia" del CNR. Firenze.
- DIETRICH, W. O., 1912, *Elephas primigenius Fraasi*, eine schwäbische Mammutrasse: Jahr. Vereins für vaterländische Naturkunde in Württemberg, 68: 42-106.
- DUBROVO, I. A., 1966, On the systematic position of fossil elephant from the Khazarsky complex: Bull. Comm. Quat. Stud., 32: 63074, Moscow (in Russian).
- , 1992, Fossil elephants from the Commonwealth of Independent States. In Agenbroad, L. D. & Mead, J. I. (eds.), The Hot Spring Mammoth Site: 426-451.
- FORLANI, E., 1987, Studio idrogeologico della conoide e fattibilità di un canale deviatore della diga sul F. Conca. Consorzio Potenziamento Acquedotto, comuni di Cattolica, Misano, Riccione (unpublished).
- KAHLKE, R.-D., 1994, Die Entstehungs-, Entwicklungs- und Verbreitungsgeschichte des oberpläistozänen *Mammuthus-Coelodonta* - Faunencomplexes in Eurasien: Abh. Senckenberg. Naturforsch. Gesellsch., 246: 1-164, Frankfurt am Main.
- KOTSAKIS, T., PALOMBO, M. R. & PETRONIO, C., 1978, *Mammuthus chosaricus* e *Cervus elaphus* del Pleistocene Superiore di Via Flaminia (Roma): Geol. Rom., 18: 411-445.
- KULCZYCKI, J., 1955, Les ossements des Mammouths: Palaeont. Polon., 7: 1-65, Warszawa.
- LISTER, A. M., 1966, Evolutionary history of mammoths in Eurasia. In Shoshani, J. & Tassy, P. (eds.), The Proboscidea: Trends in Evolution and Paleoecology: 203-213, Oxford Univ. Press.
- , & BRANDON, A., 1991, A pre-Ipswichian cold stage mammalian fauna from the Balderton Sand and Gravel, Lincolnshire, England: J. Quat. Sci., 6 (2): 139-157.
- , & JOYSEY, K. A., 1992, Scaling effect in elephant dental evolution - the example of Eurasian *Mammuthus*. In Smith, P. & Tchernov, E. (eds.), Structure, function and evolution of teeth: 185-213, Freund, Tel-Aviv.
- MUSIL, R., 1968, Die Mammutmolaren von Predmosti (CSSR): Palaont. Abhandl. Abt. A, 3: 1-192.
- NESCI, O. & SAVELLI, D., 1991, Successioni alluvionali terrazzate nell'Appennino nord-marchigiano: Geogr. Fis. Dinam. Quat., 14: 149-162.

- PALOMBO, M. R., 1972, Un cranio di *Elephas primigenius* della Via Flaminia (Roma): Geol. Rom., 11: 199-228.
- RICCI, A., 1901, L'*Elephas primigenius* nel Post-Pliocene della Toscana: Palaeontogr. It., 7: 121-148.
- ROTH, V. L., 1984, How elephants grow: heterochrony and the calibration of developmental stages in some living and fossil species: J. Vert. Paleont., 4 (1): 126-145.
- SALA, B., 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.
- SIKES, S. K., 1967, The african elephant, *Loxodonta africana*: a field method for the estimation of age: J. Zool., 154: 235-248.

(manuscript received May 23, 1997
accepted November 10, 1997)

Marco P. FERRETTI

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