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Mammuthus meridionalis (Mammalia, Proboscidea, Elephantidae) from the “Sabbie Gialle” of Oriolo (Cava La Salita, Faenza, Northern Italy) and other European late populations of southern mammoth.

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Key Words: Elephantidae, *Mammuthus meridionalis*, evolution, systematics, late Early Pleistocene, “Sabbie gialle” formation, Italy.

ABSTRACT

New finds of *Mammuthus meridionalis* from “La Salita di Oriolo” quarry (Faenza, Emilia Romagna, Italy) are described. The “Sabbie gialle” outcropping at Oriolo yielded several mammal species pointing out an early Galerian age (late Early Pleistocene) for the whole assemblage. A comparison with the type population of *M. m. meridionalis* from Upper Valdarno (Tuscany; Italy; Tasso Faunal Unit; early Early Pleistocene) and younger samples from Italy and other European localities allows to draw a possible scenario of the late evolution of the southern mammoth. On the basis of the systematic study two distinct lineages of southern mammoth are recognised. One, currently known only from Italy, is represented by several findings, among which are the Oriolo specimens and those referred to *M. m. vestinus*, characterized by large size, specialized skull and primitive dentition. A second group of forms, making its first occurrence in the early Galerian, presents instead derived dental morphology and is here referred to as *M. meridionalis* ex gr. *tamanensis*. During the middle Galerian (early Middle Pleistocene) the latter is replaced throughout Eurasia by the more evolved steppe mammoth *M. trogontherii*, a probable off-shoot of this group, while the forms belonging to the *M. m. vestinus* group became extinct without descendants.

RIASSUNTO

Sono descritti nuovi resti di *Mammuthus meridionalis* raccolti nelle “Sabbie gialle” affioranti a Cava La Salita di Oriolo (Faenza). L’associazione a mammiferi presente nei depositi di Cava La Salita è attribuibile nel suo insieme al Galeriano inferiore (parte finale del Pleistocene inferiore). Il confronto con la popolazione tipo di *M. m. meridionalis* del Valdarno Superiore (unità faunistica Tasso; parte basale del Pleistocene inferiore) e con campioni più recenti di elefante meridionale provenienti da varie località italiane ed europee, permette di ricostruire le fasi più recenti dell’evoluzione di questa specie. In base allo studio sistematico sono state riconosciute due linee evolutive. La prima, finora segnalata solo in Italia attraverso vari ritrovamenti tra cui quello di Oriolo e quelli più antichi riferiti alla sottospecie *M. m. vestinus*, comprende forme di grande taglia, cranio specializzato e dentatura primitiva. La seconda, che compare per la prima volta nel Galeriano inferiore è rappresentata dalle forme del gruppo *M. m.* ex gr. *tamanensis*, che si distinguono per i caratteri evoluti dei molari. Nel Galeriano medio (parte inferiore del Pleistocene medio) gli ultimi rappresentanti di quest’ultima linea vengono sostituiti da *M. trogontherii*, una forma più derivata e probabile discendente di questo gruppo, mentre la linea legata a *M. m. vestinus* si estingue completamente.

Introduction

Several large mammal remains were recovered from the “Sabbie gialle” outcropping at the “La Salita di Oriolo” quarry (Faenza, Emilia Romagna, Italy). The “Sabbie gialle” Formation of the north-eastern Apennine, stratigraphically overlays the Early Pleistocene “Argille Azzurre” and has been divided into two distinct sedimentary cycles by Marabini et al. (1987a, b) and Colalongo et al. (1982). According to the authors the first cycle represent the regressive closure of the marine clays, the second a minor transgressive cycle, unconformably overlying the preceding one and characterised by shore-line depositional structures. The section exposed at “La Salita di Oriolo” represents the upper part of the second depositional cycle which makes up the bulk of the “Sabbie gialle”. The fossil material, collected in several years by the personnel of the

“Museo Civico di Scienze Naturali” of Faenza, initially in collaboration with the late Dr. G. Giusberti of the “Istituto di Antropologia” of the University of Bologna, includes remains of *Stephanorhinus*, *Equus*, *Hippopotamus* and *Bison* cf. *shoetensacki* (Masini et al. 1995), besides those of the southern mammoth described in the present paper. The mammal remains were deposited in a shore-front environment near the mouth of a river, that likely transported the carcasses to the sea (Marabini et al. 1987b). Preliminary observations of the fossils, retrieved from several levels through the succession, indicate an age from latest Villafranchian to early Galerian (late Early Pleistocene). A recent magnetostratigraphic investigation performed on a 20 m section outcropping at “La Salita di Oriolo” quarry, evidenced a transition from reversed to nor-

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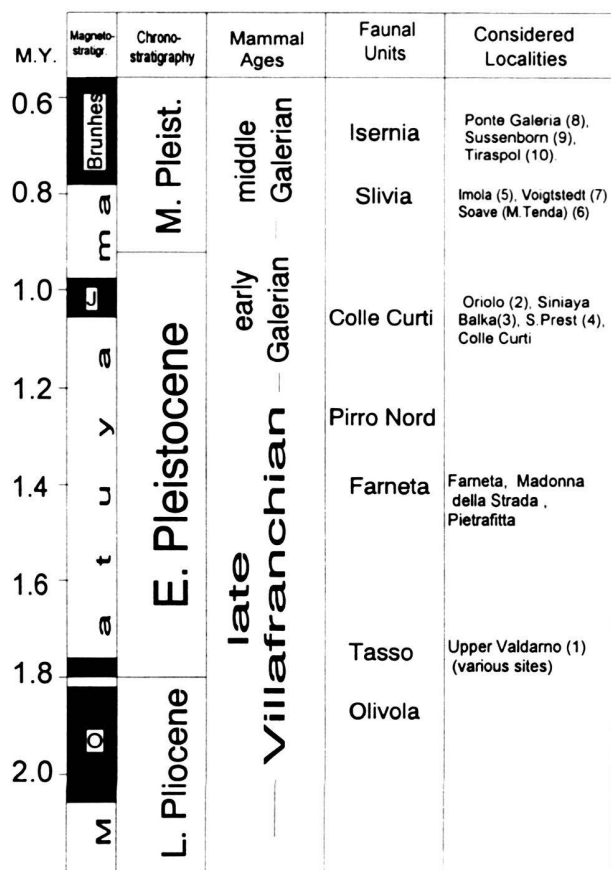


Fig. 1. Biochronological setting of the considered localities.

mal polarity in the central part of the succession (Torre et al. 1996) in agreement with the paleomagnetic data presented by Marabini et al. (1995). Part of the fauna pertains to the lower reversed interval, while the remainder, including the elephants, were retrieved from the levels above the polarity reversal, near the top of the "Sabbie gialle". However the paleomagnetic analysis does not clarify whether the paleomagnetic event should be referred to Jaramillo, as suggested by the fauna, or to the Matuyama-Brunhes transition, consistent with the "Milazzian" age (Middle Pleistocene) proposed by Vai (1984) and Marabini et al. (1987a) for the upper sequence of the "Sabbie gialle".

In the present work the remains of southern mammoth from "La Salita di Oriolo" quarry (Faenza) are described. In addition, *M. meridionalis* samples from other Italian and European late Villafranchian (Tasso and Farneta Faunal Units) and early Galerian (Colle Curti and Slivia F. U.) localities are discussed (Fig.1). Comparisons are based upon morphological and metrical characters of dentition, skull and mandible.

Abbreviations. MSNF "Museo di Storia Naturale", Faenza; IGF "Museo di Geologia e Paleontologia", Florence; MPM

"Museo di Paleontologia dell'Accademia Valdarnese del Poggio", Montevarchi; MCSNV "Museo Civico di Storia Naturale", Verona; MCICS "Museo Civico" of Imola, (Scarabelli Collection); MSN "Museo di Scienze Naturali", University of Camerino; IQW Institut für Geowissenschaften Bereich Quartärpaläontologie, Weimar.

Systematics

Order Proboscidea Illiger 1811
Family Elephantidae Gray 1821
Subfamily Elephantinae Gray 1821
Genus *Mammuthus* Brooks 1826

Mammuthus meridionalis (Nesti, 1825)

Site: "La Salita di Oriolo" (Faenza, Emilia Romagna, Italy)
Age: early Galerian (Colle Curti Faunal Unit?; late Early Pleistocene)

Material

The elephant is represented at "La Salita di Oriolo" by three specimens. The first consists in a skull with mandible and is described below. An incomplete right tibia and a fragmental rib were collected from two distinct level above that of the skull. The remains of the first individual were collected together in a single block (Fig.2). Sediment was then removed only from the upper and lateral sides of the fossil which is still partly embedded in the sandy matrix. The ventral portion of both the skull (palate and basicranium) and the mandible are, therefore, not visible at present.

Description

Skull (Fig. 3) – The skull does not show significant compressive deformations, but is heavily damaged especially on the right side (the right zygomatic arch, the dorso-lateral portion of the right premaxillary and the majority of the neuro-cranial portion, are missing) and at the level of the perinasal region, whilst the cranial vault is completely lacking. It is remarkable for its large size (Tab.1), if dental age is considered (see below). The alveolar portions of the premaxillaries (Fig. 3B) are well developed: they are long and parallel proximally but tend to flare distally. The interalveolar fossa is deep, due to the strong development of the tusks. The premaxillaries are not completely fused on the mid-line distally. Of the frontal only the uppermost part is present. This is antero-posteriorly concave and relatively narrow between the temporal crests. In lateral view the skull appears rather elongated antero-posteriorly (Fig. 3A). The zygomatic arch is robust. The large left infraorbital foramen is still obstructed by sediment. The bony process of the maxillar forming the lateral and ventral walls of the foramen is relatively thin, but well extended antero-posteriorly. Viewed from above and slightly from behind (Fig. 3C) it

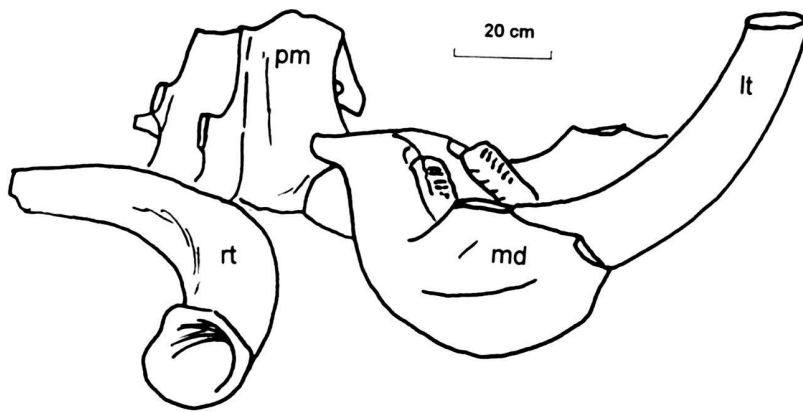


Fig. 2. Cranium and mandible of *M. meridionalis* from La Salita di Oriolo quarry (Faenza) in situ. Abbrev.: md: mandible; lt: left tusk; pm: premaxillaries; rt: right tusk.

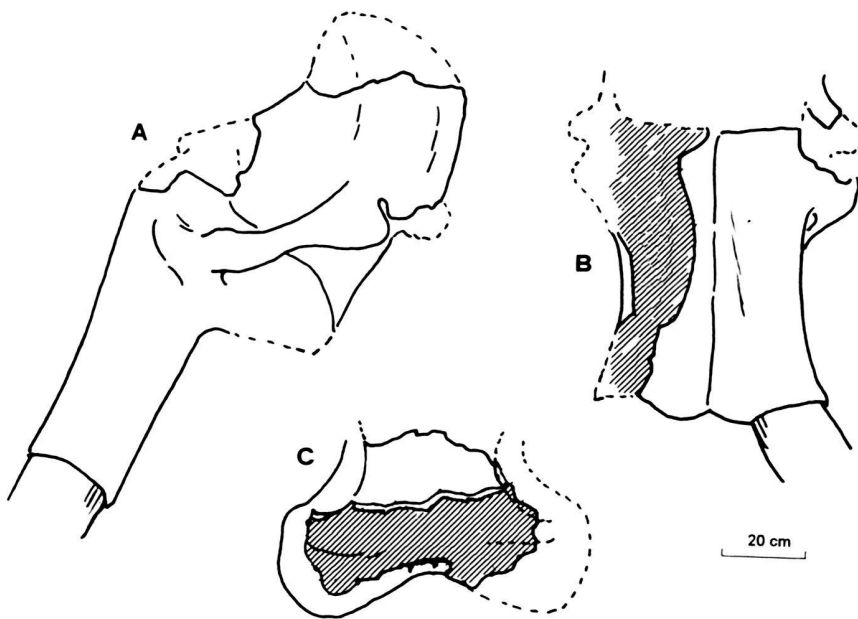


Fig. 3. Cranium of *M. meridionalis* from La Salita di Oriolo quarry (Faenza): A: left lateral side; B: anterior side; C: postero-dorsal view of the neurocranium. Proposed reconstruction of missing parts shown by dashed lines.

is possible to observe the base of the nuchal fossa, relatively narrow and with a squared section. The left portion of the neural cranium display a well developed occipital bulge. Though the upper part of the skull is not present, judging from the preserved portion, it can be argued that the position of the skull vertex should not have been so caudally displaced as in the holotype of *M. m. vestinus* (see below) but rather positioned as in the skulls of *M. m. meridionalis* (Fig. 6B) from Upper Valdarno (Tuscany, Italy, Tasso Faunal Unit, early Early Pleistocene).

Tusks – The left tusk, lacking the apex, seemingly did not undergo to any intra-alveolar rotation. It exits from the alveolus directed downward and laterally. Then it twists upwardly and, in the last portion, medially according to a pattern typical for *Mammuthus*. The maximum diameter of the left tusk, mea-

sured at its emergence from the alveolus, is 200 mm. The right tusk was found outside its sheath, along the right side of the skull (Fig. 2). The pulp cavity is visible at the proximal end. Moving apically the transverse section changes from circular to elliptical.

Mandible (Fig. 4; Tab. 2) – The mandible lacks only the condyles and the coronoid processes. The tooth in use is the M2 (see below) which does not reach the mesialmost portion of the alveolar region, where traces of the first molar alveolus are present. Very likely the M1 was already shed before the animal died. The mesialmost plates of the still unerupted M3 are visible behind the M2. The mandible presents the typical features of *M. meridionalis*. The corpus is rather long and its labial side moderately inflated. The symphysis bears a well developed beak, only moderately downwardly inclined. The as-

Tab. 1. Measurements, in millimetres, of the cranium of *M. meridionalis* from La Salita di Oriolo quarry (Faenza, Emilia Romagna, Italy) and other specimens from late Villafranchian (Tasso F.U. and Farneta F.U.) Italian localities. Measures according to von den Driesch (1976) partly modified.

Measures	Specimen						
	Oriolo MSNF c	Upper Valdarno IGF 1050	Upper Valdarno IGF 1054	Upper Valdarno IGF 1049	Scoppito (Maccagno, 1962)	Farneta IGF 15081	Farneta IGF 10957
Tooth in use	M2	M2	M3	M3	M3	–	–
1. Total length	–	–	–	1250	1540	–	–
2. Tusk alveolus length	780	507	–	715	850	920	–
3. Greatest breadth of neurocranium	–	622	863	–	–	–	911
4. Breadth of tusk alveoli between infraorbital foramina	461	412	492	491	520	595	–
5. Greatest breadth of tusk alveoli	640	425	–	–	540	635	–
6. Cranial height	–	–	874	735	–	–	–
7. Length of zygomatic arch	503	–	362	379	–	–	–
8. Maximum tusk diameter	200	83	–	188	238	–	234

Tab. 2. Measurements, in millimetres, of the mandible of *M. meridionalis* from La Salita di Oriolo quarry (Faenza, Emilia Romagna, Italy) and other specimens from late Villafranchian (Tasso F.U. and Farneta F.U.) Italian localities. Measures according to von den Driesch (1976), partly modified.

Measures	Specimen			
	Oriolo MSNF m	Upper Valdarno MPM 1	Upper Valdarno IGF 83	Scoppito (Maccagno, 1962)
Tooth in use	M2	M2	M2-M3	M3
1. Length from the angle	790	660	678	670
2. Length: infradentale-anterior origin of ascending ramus	477	362	391	440
3. Horizontal length of symphysis	110	99	127	–
4. Maximum breadth between interalveolar crests	72	76	112	–
5. Length: gonion caudale-oral border of the alveolus of the mesialmost cheektooth	569	495	540	–
6. Length: oral border of the alveolus of the mesialmost cheektooth-anterior origin of ascending ramus	292	230	266	–
7. Length: oral border of the alveolus of the mesialmost cheek-tooth-infradentale	255	210	210	–
8. Length: gonion caudale- most oral point of the anterior margin of the ascending ramus	275	–	–	320
9. Height of the mandible at midpoint of the cheektooth row	–	140	–140	190
10. Greatest thickness of the body at midpoint of cheektooth row	–163	–	–144	–
11. Breadth between the most lingual points of the <i>trigoni retro-molari</i>	267	188	270	–
12. Breadth between anterior margin of ascending rami	646	–	650	504
13. Mandibular breadth: gonion laterale-gonion laterale	551	526	540	–

ascending rami do not tend to incline medially, but are parallel. Judging from the morphology of the *incisura sigmoidalis*, the coronoid processes almost reached the level of the condyles. The anterior margins of the ascending rami, though not perfectly preserved, appears straight and not forwardly projected as in most *M.m. meridionalis* mandibles (Fig. 4 D).

Lower molars (Pl.1, Fig. 1–2) – The teeth in use are the M2 accordingly to their plate formula (PF) and occlusal breadth (FB; see Table 3 for measurements). The teeth are complete and moderately worn. They have 11 plates, the first 10 in use. The occlusal surface is narrow, with a maximum diameter (FB)

of 73 mm. Only the first 3–4 plates show a complete enamel loop, while the following ones are still divided into rings. In particular the central plates tend to form three rings of sub-equal size. The enamel is rather thick and forms few rounded folds.

The characters displayed by the Oriolo elephant clearly point out to *M. meridionalis*. According to the tooth in use, the overall size and robustness of the tusks it probably represents an adult male in its prime. The position of the Oriolo specimen with respect to the various recognised subspecies of the southern mammoth is discussed further below.

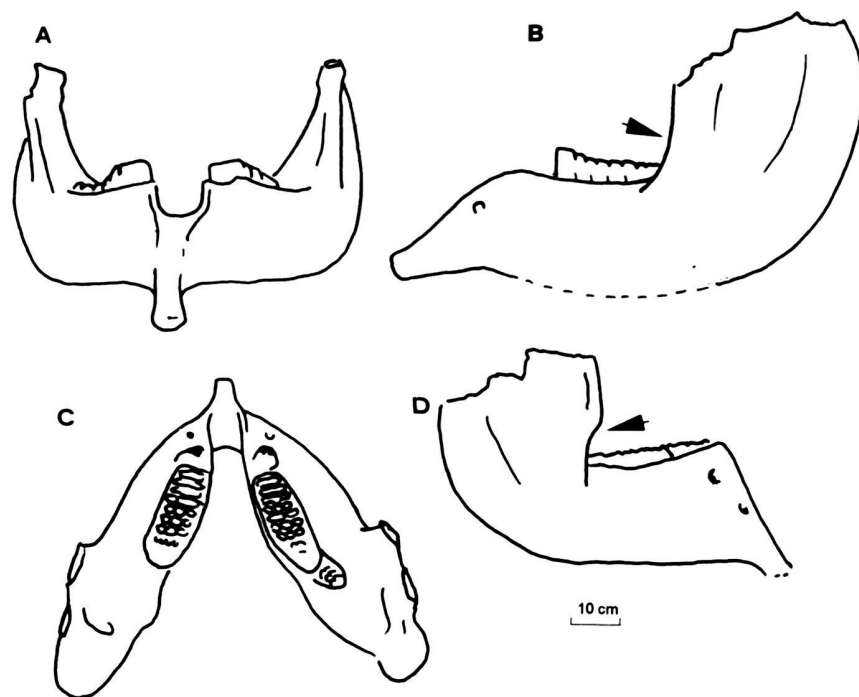


Fig. 4. Mandibles of *M.meridionalis*. Mandible from La Salita di Oriolo quarry (Faenza) A: anterior view; B: left lateral view; C: occlusal view. Mandible of *M.m.meridionalis* (IGF 53) from Upper Valdarno, Italy D: lateral view. Arrows highlight the different shape of the anterior margin of the ascending ramus in the Oriolo and Upper Valdarno mandibles.

Other Italian late Villafranchian (Farneta Faunal Unit) and early Galerian (Colle Curti and Slivia F.U) *M.meridionalis* finds

M. meridionalis vestinus (Azzaroli 1972)

Sites: Madonna della Strada, near Scoppito (L'Aquila, Abruzzo); Farneta (Val di Chiana, Toscana)

Age: Late Villafranchian (Farneta Faunal Unit), Early Pleistocene; (Azzaroli 1977; Azzaroli et al. 1988)

Azzaroli (in Ambrosetti et al. 1972; 1977) attributes an almost complete skeleton from Madonna della Strada near Scoppito (L'Aquila, Abruzzi), already described by Maccagno (1962) as "*E.meridionalis*", to a new subspecies of southern mammoth *M.meridionalis vestinus*, for its derived cranial morphology and very large size, even though it does not differ from the type form from Upper Valdarno as regards dental characters. Azzaroli (1977) assigns to *M.meridionalis vestinus* also the elephants remains from the surrounding of the Abbey of Farneta in the Chiana Valley. The material, housed in the paleontological museum of Florence (IGF), includes two fragmented skulls, isolated molars, post-cranials and a partial skeleton belonging to an old individual. This with some other specimens are very large sized, in some cases exceeding the size range observed in *M.m.meridionalis* from Upper Valdarno. On the other hand molars are morphologically and metrically fully comparable with those of the latter subspecies.

The Scoppito skull was found heavily damaged, particularly in the fronto-parietal region (Maccagno 1962) and thus its morphology should be evaluated with caution. More reliable is

one of the cranial remains from Farneta (IGF 10957), better preserved and only slightly deformed. It consists of the brain case which shows a strong vertical development, very concave frontals and laterally bulging parietals (Fig. 5 A–B;). These characters match with the diagnosis of *M.m.vestinus* proposed by Azzaroli (1977).

M. meridionalis cf. *vestinus*

Site: Pietrafitta (Perugia, Umbria)

Age: Late Villafranchian (Farneta Faunal Unit, Early Pleistocene; Ficarelli et al. 1996; Gentili et al. 1996).

The numerous elephant remains collected from the lignite of Pietrafitta, housed in the premises of the local E.N.E.L. mine, have been referred to *M.m.vestinus* by several authors (Torre et al. 1992; Gentili et al. 1996). However such an attribution, led partly by the supposed equivalent ages of the Scoppito and Pietrafitta faunas, cannot be definitively confirmed until the skulls retrieved from this locality are restored. Concerning the dental characters, the Pietrafitta population falls, both morphologically and metrically, within the range of variability observed in the Upper Valdarno sample (Tab.4), except for slightly thinner enamel and smaller coronal width means in the upper and lower M3. This last character determines slightly higher hypsodonty index (K:GH/GB) values. Such differences actually make the Pietrafitta M3 more progressive than those from Upper Valdarno. The M1 and M2 are, on the contrary, more conservative. The only evidence that could indicate *M.m.vestinus* is the extremely large size of some long bones and tusks from this site (Ferretti 1997).

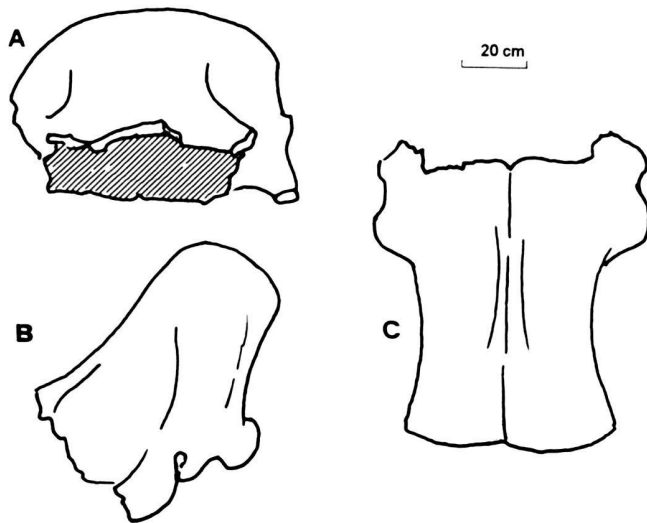


Fig. 5. Cranium and premaxilla (tusk alveoli) of *M.m.vestinus* from Farneta (Val di Chiana, Italy). Cranium (IGF 10957) A: anterior view; B: left lateral view; premaxilla (IGF 15081) C: anterior view.

Mammuthus sp.

Site: Colle Curti (Colfiorito basin, Macerata, Marche)

Age: early Galerian (Colle Curti F.U.), late Early Pleistocene (Ficcarelli & Silvestrini 1991; Torre et al. 1996)

The few elephant remains collected from Colle Curti (Colfiorito Basin, Macerata) in the Umbro-Marchean Apennine, very likely belong to a single individual. The material consists of a fragmentary tusk, two dorsal vertebrae, two ribs and the incomplete shafts of an humerus and a femur. The animal was not fully mature as demonstrated by the not yet completed ossification of vertebrae and ribs. Consistently the tusk, consisting only of the proximal extra-alveolar portion, seems to pertain to a juvenile individual even if it could also represent a small female. This is the only element for a systematic diagnosis. The section is elliptic. The evident torsion of the longitudinal axis and the flattening of the dorso-lateral side are both mammothine characters. In this features both *M.meridionalis* and *M.trogotherii* are very similar. However the first occurrence of the latter species is attested only from association younger than Colle Curti, while the presence of various "Villafranchian" taxa in the Colle Curti assemblage (Ficcarelli & Mazza 1990; Ficcarelli et al. 1996) would make an attribution to *M.meridionalis* more likely.

M.aff. meridionalis (evolved form)

Site: Rio Pradella, "Sabbie gialle" formation, Imola (Emilia Romagna)

Age: middle Galerian (Slivia F.U.), early Middle Pleistocene (Azzaroli & Berzi 1970; Masini et al. 1995)

Among the large mammals remains of the so called "Sabbie gialle" of Imola fauna elephants are represented by an evolved *M. meridionalis* form (Azzaroli & Berzi 1970; Masini et al. 1995). In particular one upper and one lower M3, probably belonging to the same individual, are characterised by elevated plates number (16 including talons), relatively thin enamel (2,6 mm) and high hypsodonty index (Tab. 3). The small dimensions of the two teeth is partly responsible of the high lamellar frequency index (DLI), computed as the quotient between number of plates and greatest mesio-distal length (GL; cf. Lister & Joysey 1992). Particularly progressive is the occlusal surface morphology characterised by narrow enamel loops (Pl.1, Fig.4). The Imola fauna is typical of the early middle Galerian (early Middle Pleistocene) and derives from, at least, three levels. The two M3 likely pertain to the most recent one (Masini et al. 1995). The molars were assigned to *M.cf. meridionalis* by Azzaroli & Berzi (1970) who considered them similar to the "mutation cromerense" created by Depéret & Mayet (1923) for some molars from the Cromer Forest Bed formation and from various coeval French localities. Nonetheless, given the present state of knowledge (see below), the Imola elephant can be reasonably determined only as *M. aff. meridionalis* (evolved form).

M.cf. meridionalis

Site: Soave, Monte Tenda (Verona, Veneto)

Age: middle Galerian (Slivia F.U.), early Middle Pleistocene (Masini et al. 1994)

The elephant molars from this locality (Tab. 3) have been referred to *M.trogotherii* by Masini et al. (1994), and regarded as the probable first occurrence of this species in Italy by Palombo (1994).

However, even though the fragmentary state and paucity of the material do not allow a satisfactory attribution, they seem to fit better an attribution to *M.meridionalis*. In particular one upper M2 (MCSNV 10688) from Soave is almost complete and displays the typical characters of the southern mammoth (Tab. 3). None of the teeth present particular derived features.

Evolved *M.meridionalis* populations from various European localities

Various *M.meridionalis* samples from late early Pleistocene and early middle Pleistocene European localities display advanced characters, mostly in dental morphology, respect to the type population from Upper Valdarno and accordingly are regarded by some authors as separate subspecies. Some of them are discussed below and compared to the Italian findings previously described.

Tab. 3. Measurements, in millimetres, of *M. meridionalis* molars from various Italian localities. GL = greatest mesio-distal length; FL = occlusal length; GB = greatest bucco-lingual breadth; FB = occlusal breadth; GH = greatest height; PF = plate formula (including talons); DLI = lamellar density index (PF/GLx100); Q = functional lamellar index (U/FL x 100); K = hypsodonty index (GH/GB).

Locality	Specimen	Tooth	GL	FL	GB	FB	GH	PF	U	ET	DLI	Q	K
La Salita di Oriolo	MSNF r	M/2 right	–	172	–	72	–	11	10	3.0	–	5.5	–
	MSNF l	M/2 left	–	169	82	83	–	11	10	3.0	–	5.6	–
Soave (M.Tenda)	MSNV 10688	M/2 right	206	–120	90	76	115	12	8	3.0	5.8	–6.6	1.3
	MSNV 222	M/3?	–	–	–87	–	126	>5	–	3.0	–	–	–
	MSNV 221	M lower	> 49	–	84	–	–	>3	–1.9	6.1	–	–	–
	MSNV 12288	M/3 right	>160	–	105	–	122	>6	–	3.1	3.8	–	–
Imola (Rio Pradella)	MCI 7644	M/3 left	235	120	90	83	158	16	7	2.4	6.6	5.8	1.8
	MCI 7645	M/3 left	–255	–163	91	89	120	–14	9	2.6	5.5	5.5	1.3

M. meridionalis voigtstedtensis (Dietrich 1958)

Locality: Voigtstedt (Thuringia, Germany)

Age: middle Galerian, early Middle Pleistocene (Kahlke 1965; Azzaroli et al. 1988; Maul 1990)

Dietrich (1958, 1965), in his description of the elephants molars from Voigtstedt (Thuringia, Germany) pointed out their intermediate characters between *M. meridionalis* and *M. trogontherii*, concluding they belong to an evolved subspecies of the former, which he names *M. meridionalis voigtstedtensis*. The teeth, like most of the Voigtstedt-Edersleben fauna probably derive all from the same level, namely the “Lehmschicht”, that according to German authors correlates to the beginning of the Brunhes paleomagnetic epoch (Kahlke 1965; Wiegank 1981; Maul 1990; Kahlke & Mania 1994). The sample displays a large amount of variability (Tab. 4), in part due to the low number of specimens representing each tooth category and to their fragmentary state, but indeed could be consistent with the possibility it represents a transitional form. Some of the Voigtstedt molars actually do not differentiate from that of Upper Valdarno. Some others, though still morphologically similar to the latter, are derived in some characters as hypsodonty and lamellar frequency. Finally, a few of the teeth fall within the variability range of *M. trogontherii* (Tab. 4).

M. m. tamanensis (Dubrovo 1964)

Site: Siniaya Balka (Taman peninsula, Russia)

Age: early Galerian, late Early Pleistocene (Vangengeim et al. 1991)

M. meridionalis tamanensis is characterised by having quite hypsodont molars and by M3 possessing, on the average, a higher number of plates than the type population from Upper Valdarno (Dubrovo 1992; Lister & Joysey 1992; Lister 1996a; Tab.4). Differences in enamel thickness and lamellar frequency are, however, less significant. The type specimen of *M. m. tamanensis*, a female skull with mandible (Dubrovo 1964),

shows that no particular morphological modification occurred in the time interval that separates the two samples.

M. m. depereti (Coppens & Beden 1982)

Site: Saint-Prest (Eure-et-Loire, France)

Age: early Galerian, late Early Pleistocene (Bonifay 1969; Coppens & Beden 1982; Azzaroli 1983)

Coppens & Beden (1982) erected the subspecies *M. m. depereti* for the elephant material from Saint Prest (Eure-et-Loire, France), previously described as “*E. meridionalis* “mutation de Saint-Prestien” by Deperet & Mayet (1923). Coppens & Beden (1982) do not report the means of the dental variables they measured, but only their observed range without distinguishing between upper and lower molars. This makes comparisons with other samples uncertain. The new subspecies seems to be characterised by a somewhat smaller tooth size and by an increased plate number compared to typical *M. meridionalis* (Tab. 4). It distinguishes from *M. m. tamanensis* in maintaining a relatively low crown. Less clear is whether the mammoth from Saint-Prest is also differentiated in its enamel thickness with respect to *M. meridionalis* from Upper Valdarno. The ranges given by the two French authors for M2 and M3 are shifted toward lower values compared to the Upper Valdarno sample, but this could be related to the smaller size of the Saint-Prest specimens.

The elephant material from the Cromer Forest-bed Formation outcropping at Kessingland (Norfolk, East Anglia) was ascribed by Pontier (1908) and then by Deperet & Mayet, (1923) to an evolved form of the southern mammoth, named thereafter *M. m. cromerensis* by Osborn (1942). A recent revision of the material from the Cromer Forest bed revealed, however, that the species represented at Kessingland is the more evolved *M. trogontherii* (Lister 1996b, 1998 pers. com.).

Recently Malez & Lenardic-Fabic (1988) described a new subspecies of southern mammoth, *M. m. adriaticus*, on the basis of an upper M3 and a femur shaft, collected from the sea bottom between the isles of Rab and Lagging in the northern

Tab. 4. Descriptive statistics of the biometric parameters of the M2 and M3 of the various *M. meridionalis* populations considered and of *M. trogontherii* from Süssenborn (Germany, middle Pleistocene). u = upper molars; l = lower molars; N = number of specimens.

Species/Locality	Tooth	Breadth (GB)			Plate Formula ^a			Enamel Thickness			Frequency Index ^b			Hypsodonty Index ^c		
		N	Mean	Range	N	Mean	Range	N	Mean	Range	N	Mean	Range	N	Mean	Range
<i>M.meridionalis</i>																
Upper Valdarno	M3 u	29	101	83–123	27	14	11–16	33	3.2	2.6–3.9	24	5.4	4.3–6.2	13	1.3	1.0–1.6
	l	12	91	81–113	19	14	12–16	19	3.0	2.4–3.7	10	5.1	3.9–5.9	6	1.3	1.0–1.6
	M2 u	15	89	80–103	15	11	10–12	17	2.7	2.2–3.4	14	5.2	4.5–5.9	11	1.4	1.1–1.6
	l	3	83	82– 86	4	11	11–11	3	2.8	2.7–2.9	3	5.4	5.3–5.6	3	1.3	1.2–1.3
Pietrafitta	M3 u	4	93	84–103	3	14	13–16	4	2.9	2.6–3.3	2	5.4	4.4–6.5	3	1.4	1.3–1.5
	l	5	85	75– 94	6	14	12–15	6	2.9	2.7–3.1	2	5.3	5.0–5.7	1	1.3	–
	M2 u	4	84	73– 95	4	11	8–12	3	2.7	2.6–2.9	3	5.4	4.8–5.8	2	1.3	1.2–1.4
	l	2	90	84– 96	2	11	10–12	3	2.9	2.6–3.0	2	5.3	4.4–6.2	2	1.2	1.0–1.4
Saint Prest ¹	M3	10	–	88–105	10	–	15–17	10	–	2.4–3.7	10	–	4.6–6.1	10	–	1.1–1.4
	M2	10	–	74–102	10	–	10–11	10	–	2.3–3.5	10	–	4.7–6.6	–	–	–
Siniaya Balka ²	M3 u	12	104	85–115	5	18	16–20	12	3.0	2.2–4.0	12	5.8	4.7–6.7	5	1.5	1.3–1.8
	l	–	–	82–122	–	18	16–20	–	–	2.5–4.0	–	–	4.0–6.0	–	–	–
	M2 u	–	–	–	–	–	11–15	–	–	–	–	–	4.5–6.5	–	–	–
	l	–	–	–	–	–	11–15	–	–	2.0–3.5	–	–	4.0–6.5	–	–	–
Voigtstedt	M3 u	2	91	75–107	1	15?	–	2	3.3	3.0–3.6	2	6.7	6.6–6.8	2	1.4	1.3–1.5
	l	3	95	95– 96	1	15	–	2	2.9	2.7–3.2	1	5.0	–	2	1.4	1.3–1.5
	M2 u	1	76	–	1	>12	–	1	1.8	–	1	10.0	–	–	–	–
	l	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>M.trogontherii</i>																
Süssenborn	M3 u	47	97	82–116	45	20	15–23	46	2.3	1.9–3.0	48	7.7	5.5–9.1	43	1.8	1.3–2.3
	l	40	94	73–114	36	19	15–23	42	2.3	2.0–2.9	40	5.6	4.4–7.0	34	1.6	1.3–2.3
	M2 u	23	85	68–103	20	15	13–16	17	2.0	1.6–2.4	23	7.5	6.2–8.3	19	1.9	1.3–2.2
	l	10	72	65– 82	9	15	13–17	10	1.9	1.5–2.2	10	7.4	6.3–9.1	9	1.7	1.6–2.0

^a Including talons

^b Lamellar frequency index (DLI), according to Adam, (1953).

^c Hypsodonty index (K), according to Aguirre, (1968).

¹ Data from Coppens & Beden, (1982).

² Data from Dubrovo, (1964), Lister and Joysey, (1992) and Lister, (1996a).

Adriatic sea. However, from the figures and the measurements given by the authors, an attribution to *Elephas (Palaeoloxodon) antiquus* is more likely, as already suggested by Palombo (1994).

Discussion

The primitive dental characters of the Oriolo mammoth seem to exclude the possibility that it belongs to one of the derived subspecies of southern mammoth such as *M. m. tamanensis*. On the other hand the large size, the particular morphology of the mandible and the cranial features, would not exclude a relationship of the Oriolo mammoth with *M. m. vestinus*.

In order to try to clarify the systematic position of the Oriolo elephant and its relationships with the various populations of southern mammoth so far considered, the major morphological changes which characterized the evolution of *M. merid-*

ionalis from the latest Villafranchian to the late early Galerian are discussed.

Size change – Changes in size are better detected on cranial and post-cranial remains than on teeth. However the scanty material at our disposal suggests caution with the comparisons. Samples younger than that from Upper Valdarno, which represent the typical form, seem to have undergone to an increment in overall size. The Pietrafitta population, which represents one of the richest samples, is characterised by greater dimension of the tusks, long bones and vertebrae, but carpal bones, which are best represented elements, do not differ from the values of the Upper Valdarno sample (Ferretti 1997). The largest among the Italian specimens of *M. meridionalis* are those referred to the subspecies *vestinus* belonging to the Farneta F.U (late Villafranchian). The specimen from Oriolo, which is more recent than the Farneta F.U., also displays large

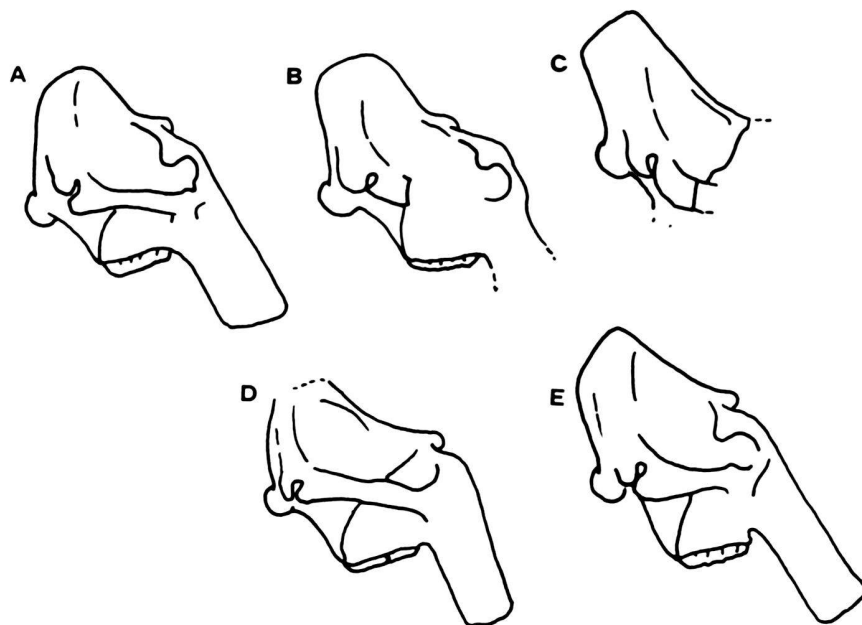


Fig. 6. Modification of the cranium in the European *Mammuthus* lineage. A: *M.gromovi*, Liventsovka, Russia (Middle Pliocene; redrawn from Garutt & Bajguseva, 1981); B: *M.meridionalis*, Upper Valdarno, Italy (Tasso F.U.; early Early Pleistocene.); C: *M.m.vestinus* (reversed), Farneta, Italy (Farneta F.U., middle Early Pleistocene); D: *M.m.tamanensis*, Siniaya Balka, Russia (late Early Pleistocene; redrawn from Dubrovo, 1964); E: *M.trogontherii chosari-cus*, Tarquinia, Italy (late Middle Pleistocene; redrawn from Ambrosetti, 1964).

size. *M.m.voigtstedtensis* post-cranial is not known. However *M.m.tamanensis*, which is a closely related form, seems also characterised by a large body size (cf. Azzaroli 1977). *M.m.depereti* is known only from teeth and few mandibles. According to the measurements on the molars this form should have been similar or slightly smaller than *M.m.meridionalis*, a characteristic which separates this subspecies from the other late *M.meridionalis* samples so far considered. A trend toward a larger size would be consistent with the very large dimension of *M.trogontherii*, the supposed descendant of *M.meridionalis*. The few skeletons referred to *M.trogontherii* (Lister 1996a) and the type material from the middle Pleistocene site of Süssenborn, Germany (Ferretti 1997), show in fact that this species was somewhat larger than *M.m.meridionalis*.

Skull/mandible morphology – Complete skulls of *M.meridionalis* are extremely rare. Moreover one has to account for the great variability in cranial morphology occurring in elephants between immature and adult, male and female. Also poorly known is the skull of *M.trogontherii*. However, the general trend displayed by the genus is toward an antero-posterior shortening of the neural portion of the skull, an anterior shift of the vertex and a flattening of the fronto-parietal region (Maglio 1973; Fig. 6). The premaxillaries became more and more slender and downward pointing along with the relative reduction of the diameter of the tusk. The Italian material referred to *M.m.vestinus* shows instead a trend which emphasises the “meridionaloid” pattern: i.e. further posterior displacement of the skull vertex, forefront very concave, parietal domes extremely expanded, skull antero-posteriorly elongated (Azzaroli 1977; Fig. 5 A-B; Fig. 6 C). Premaxillaries are some-

what proportionally slender, but the tusks became enormous. The skull from Oriolo shows a typical *M.meridionalis* morphology and in the shape of the premaxillaries it resembles *M.m.vestinus* (Fig. 5 C). A complete skull of *M.m.tamanensis* is unknown except for the holotype, which is rather crushed and belongs to a relatively young specimen, probably a female (Dubrovo 1964). Its morphology does not show significant differences respect the skulls from Upper Valdarno (Fig. 6B, D). Mandibles of *M.meridionalis* are better represented. The numerous mandible from Pietrafitta and that of *M.m.tamanensis* (Dubrovo 1964) agree with those of the typical form from Upper Valdarno and are characterized by a long and slender corpus, and a well developed beak. Characteristically moreover the anterior margin of the ascending ramus, where the temporal muscle inserts, is antero-posteriorly expanded in its upper half (Fig. 4D). Differently the mandible of *M.m.vestinus* from Scoppito and that of the Oriolo specimen possess a straight anterior margin (Fig. 4B). In *M.trogontherii* and *M.primigenius* the expanded portion tends to reduce, thanks also to a progressive dorsal shift of its base. The occurrence of this derived morphology in *M.m.vestinus* is in contrast with the evolution of the skull, that seems to specialize in a direction not leading to *M.trogontherii* (Fig. 6E). However the sample from Pietrafitta, referred to *M.m. cf. vestinus*, would demonstrate the rarity of the derived morphotype within this subspecies.

Dental evolution – On the basis of dental characters *M.meridionalis* samples younger than the Tasso F.U. can be divided into two groups. One is formed by *M.m.vestinus*, the Oriolo specimen and probably the sample from Monte Tenda

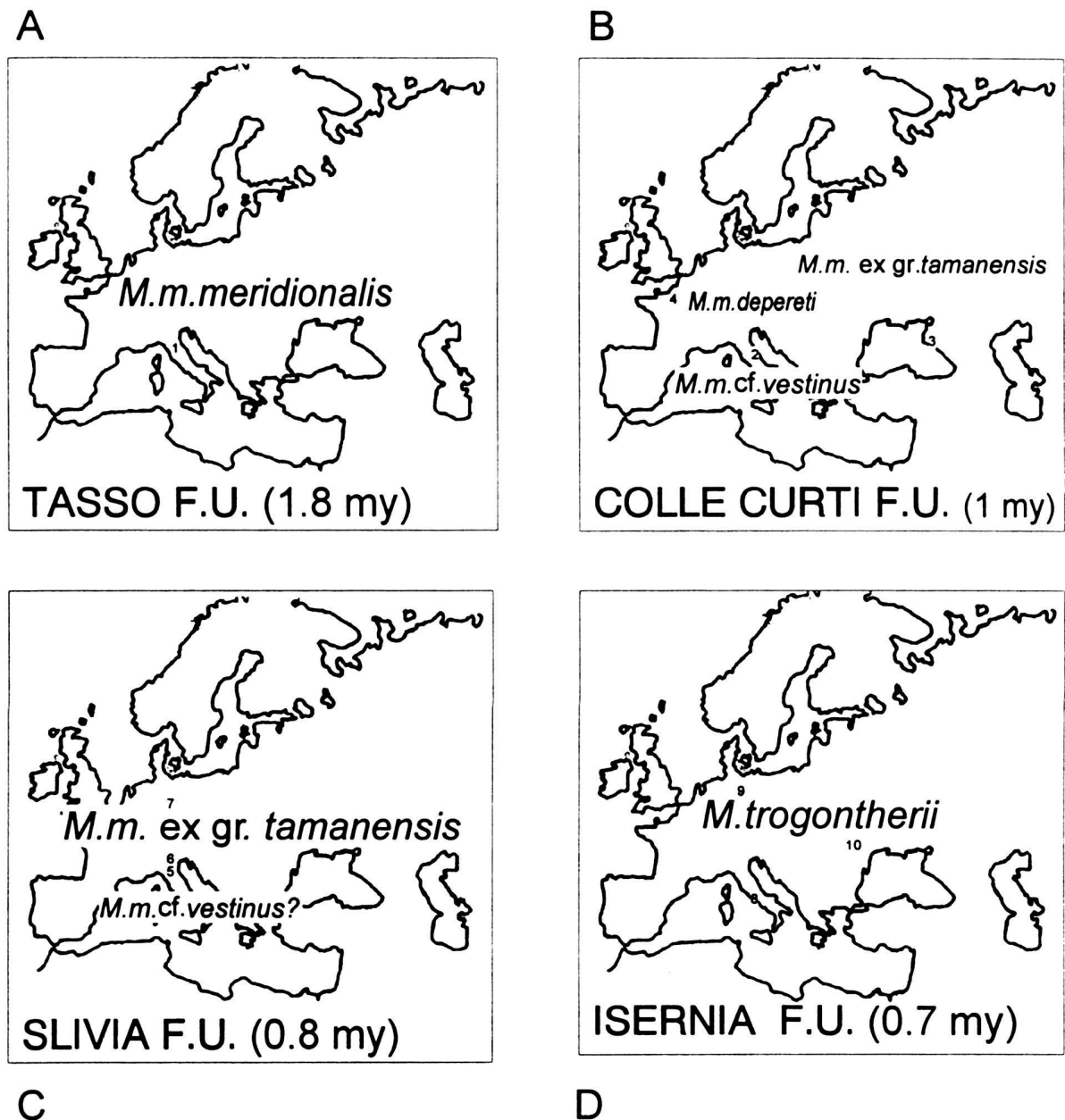


Fig. 7. Proposed evolutionary and distributional pattern of the *M. meridionalis*-*M. trogontherii* lineage in Europe from early Pleistocene (Tasso F.U.) to middle Middle Pleistocene (Isernia F.U.). The four maps also show the distribution of the main localities discussed in the text, according to their age: 1: Upper Valdarno; 2: Oriolo; 3: Siniya Balka; 4: Saint Prest; 5: Imola; 6: Soave (Monte Tenda); 7: Voigtstedt; 8: Ponte Galeria; 9: Süssenborn; 10: Tiraspol.

(Soave). This group does not show any marked tendency to increment in plate number and hypsodonty, but retains the primitive condition. A second group is represented by *M.m. tamanensis* and *M.m. voigtstedtensis*. The material from Imola, here referred to *M. cf. meridionalis* (evolved form) probably belongs to such a group. These latter forms are derived in pos-

sessing more hypsodont molars bearing a greater number of plates. With respect to these characters *M.m. tamanensis* and *M.m. voigtstedtensis* are intermediate between *M.m. meridionalis* and *M. trogontherii*. *M.m. depereti* is close to *M.m. meridionalis* and *M.m. vestinus*, but is slightly more progressive in its plate formula. It could represent both a first differentiation

from *M.m.meridionalis* toward the *M.m.tamanensis* group of forms, or an independent form from north-western Europe. In general the M3 are the teeth which seems to evolve more rapidly, but this does not constitute the rule, as in some cases the intermediate molars, mostly M1 and M2, are more progressive. The pattern of change in the means of biometric parameters in the passage from *M.m.meridionalis* to the form related to *M.m. tamanensis* is patchy. This is particularly evident in the trend of reduction of the enamel thickness (ET; Tab. 4). In fact in some cases a decrease of the average of ET is reached through the loss of the morphotype which displays the most elevated values (e.g. Voigtstedt), while in others the entire range shifts toward lower values (e.g. Saint Prest). In a third case only the minimum is lowered (e.g. Siniaya Balka).

Conclusions

As a result of the present systematic study a preliminary picture of the final evolution of European *M.meridionalis* can be drawn (Fig. 7). From a systematic point of view, while in the first part of the late Villafranchian (Tasso F.U.) all the fossil material from Eurasia seems ascribable to *M.m.meridionalis* (Fig. 7A), at the beginning of the Galerian (Colle Curti F.U.) two distinct groups can be recognised (Fig. 7B). One, currently known only from Italy, is represented by various findings, among which are the Oriolo specimens, and is characterised by large size and primitive dentition. This form could indeed represent the descendant of *M.m.vestinus* from the latest Villafranchian (Farneta F.U.) of Italy. A second group of forms making its first occurrence in the early Galerian (Colle Curti F.U.), presents instead derived dental morphology together with a comparable increment in body size. It includes *M.m.tamanensis* and *M.m.voigtstedtensis*, which according to their characters may actually represent a single taxon. This was already suggested by Maglio (1973) who grouped this forms in his *M.meridionalis* Bacton Stage. However, as pointed out by Lister (1996a) the material from Bacton, in particular a complete skull, does not show particularly derived characters. *M.meridionalis tamanensis*, is, on the other hand, surely derived in its dental characters and is well documented by abundant dental and skeletal material at Siniaya Balka (Russia) and by two almost complete skeletons from the C.S.I (Garutt 1954; Garutt & Safronov 1965). For these reason I propose to group these subspecies under the name *M.meridionalis* ex gr. *tamanensis* in order to stress their strong affinity until their systematic position is not definitely clarified. *M.meridionalis* ex gr. *tamanensis* was widespread through north-eastern Europe and possibly northern Asia (Vislobokova et al. 1995). It probably represents a form adapted to a more open biotope than those occupied by *M.m.meridionalis* and *M.m.vestinus*, and its diffusion seems to be related to the strong climatic deterioration which produced, at the end of the early Pleistocene, the faunal renewal which marks the transition from the Villafranchian to the Galerian Mammal Ages (Azzaroli et al. 1988; Gliozzi et al. 1997). At the beginning of the middle Galerian (Slivia F.U.;

Fig. 7C), *M.meridionalis* ex gr. *tamanensis* entered Italy, as it is documented by the Imola specimens, and is recorded also from Spain (Aguirre & Morales 1990) and the Levant (Tchernov & Shoshani 1996). On the other hand the Monte Tenda (Soave) findings could demonstrate the survivorship in Italy of the phyletic line related to *M.m.vestinus* up to the Slivia F.U. (Fig. 7C). These are probably the last occurrence of *M.meridionalis* in Europe, which is replaced, in younger deposits, as Süssenborn in Germany, Tiraspol in Moldova (Dubrovo 1975) and Ponte Galeria in Italy (Ambrosetti 1967), by *M.trogontherii* (Fig. 7D), which probably originated from a population of the *M.m.tamanensis* group.

Postscriptum: In a recent article by Amorosi et al. (1998), the middle Pleistocene shallow marine deposits cropping out in the northern Apennines piedmont area, traditionally known as "Sabbie Gialle" (yellow sands), have been formally described and named Imola Sands.

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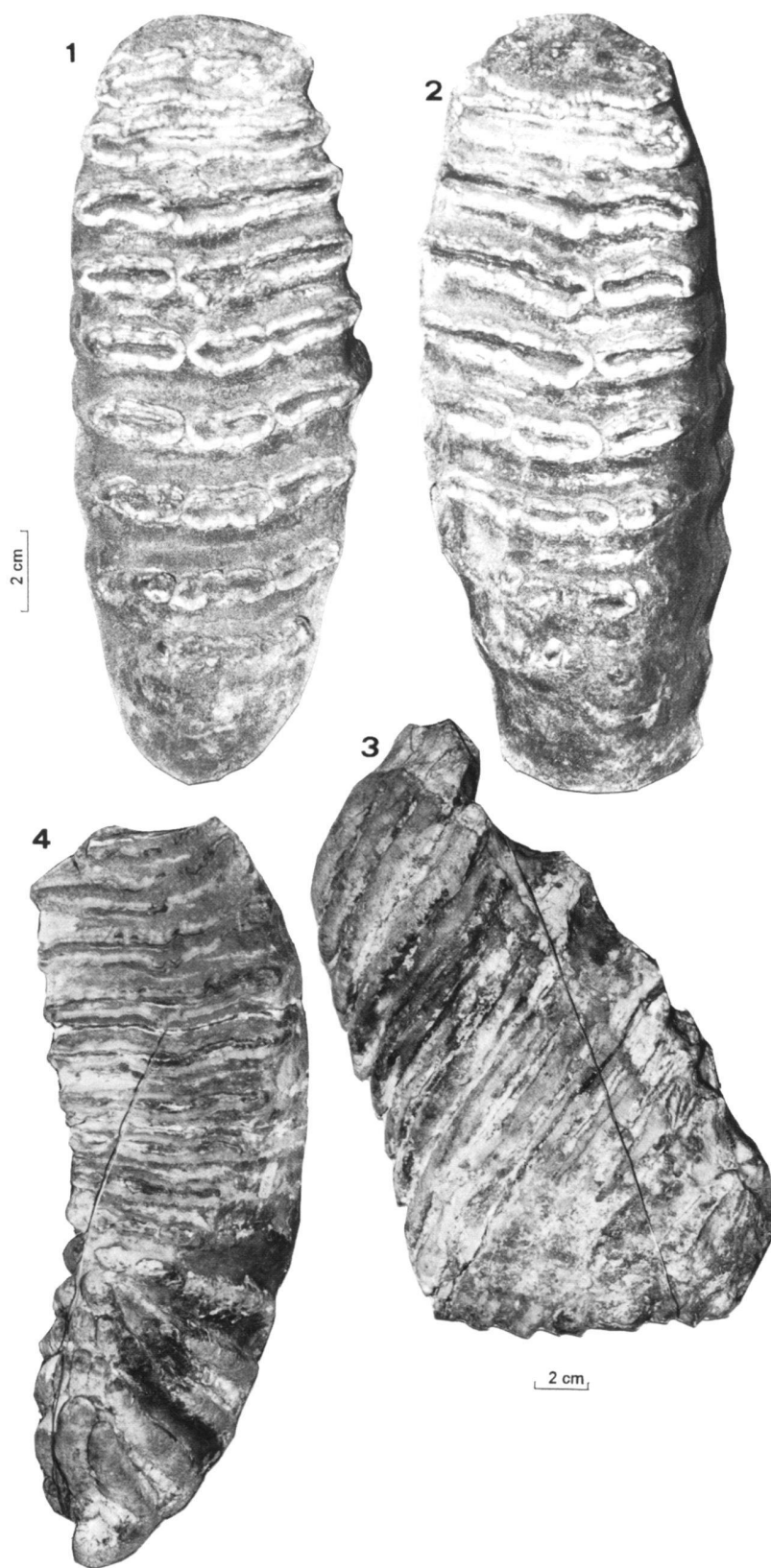


Plate 1

Fig. 1. *M. meridionalis* from La Salita di Oriolo quarry (Faenza). Lower right M2, occlusal view.

Fig. 2. *M. meridionalis* from La Salita di Oriolo quarry (Faenza). Lower left M2, occlusal view.

Fig. 3. *M. aff. meridionalis* (evolved form) from Imola (Bologna, Italy). Upper left M3, lingual view.

Fig. 4. *M. aff. meridionalis* (evolved form) from Imola (Bologna, Italy). Lower left M3, occlusal view.

