

Biochronology and palaeoenvironmental changes from the Middle Pliocene to the Late Pleistocene in Central Italy

Carmelo PETRONIO

Luca BELLUCCI

Dipartimento di Scienze della Terra, "Sapienza", Università di Roma,
Piazzale A. Moro, 5, IT-00185 Roma (Italy)
carmelo.petronio@uniroma1.it
lbellucci78@gmail.com

Edoardo MARTINETTO

Dipartimento di Scienze della Terra, Università di Torino,
via Valperga Caluso, 35, IT-10125 Torino (Italy)
edoardo.martinetto@unito.it

Luca PANDOLFI

Leonardo SALARI

Dipartimento di Scienze della Terra, "Sapienza", Università di Roma,
Piazzale A. Moro, 5, IT-00185 Roma (Italy)
leonardosalari@virgilio.it
l.pandolfi@yahoo.it

Petronio C., Bellucci L., Martinetto E., Pandolfi L. & Salari L. 2011. — Biochronology and palaeoenvironmental changes from the Middle Pliocene to the Late Pleistocene in Central Italy. *Geodiversitas* 33 (3): 485-517. DOI: 10.5252/g2011n3a4.

ABSTRACT

Paleoenvironmental variations that occurred in Italy from the Middle Pliocene to the Late Pleistocene are described. The number of large mammal species seems increased moderately, especially from the Galerian to the Late Aurelian biochronological units. On the contrary, the paleobotanical data show a decrease of the forest cover from the Middle Pliocene to the late Early Pleistocene and an increase of lands occupied by prairies and steppes. This change is also supported by the appearance of hypsodont taxa among mammals. The distribution of mammal faunas between the Adriatic and Tyrrhenian sides of Central Italy, during the Middle and Late Pleistocene, seems not to be influenced by climatic and environment differences. When the Adriatic data are more complete, it is possible, in fact, to observe a trend that is fairly close to that of the Tyrrhenian. The majority of megaherbivorous taxa has an Asian origin, and it can be hypothesized that in the interglacial phases, the Tosco-Emilian Apennines allowed the taxa coming from the northeast to enter and spread out into the more diversified Tyrrhenian side, whereas during the glacial periods the

KEY WORDS

Biochronology,
Italy,
Pliocene,
Pleistocene,
large mammals.

narrow Ligurian corridor were followed. This research supports the role of the Italian Peninsula as a refuge area for continental Europe; this particular condition permits the Italian mammal faunas to develop endemic lineage (such as *Elephas antiquus italicus* Osborn, 1931, *Cervus elaphus rianensis* Leonardi & Petronio, 1974, *C. e. aretinus* Azzaroli, 1947, etc.). At last, biodiversity sharply dropped during the last 30 000 years, probably due to the anthropic activities and the strong climatic cooling of the last pleniglacial.

RÉSUMÉ

Biochronologie et variations paléo-environnementales en Italie centrale du Pliocène moyen à la fin du Pléistocène.

Les variations paléo-environnementales qui ont eu lieu en Italie du Pliocène moyen au Pléistocène supérieur sont décrites. Il semblerait que le nombre des espèces de mammifères de grande taille ait peu augmenté, surtout pour les unités biochronologiques du Galérien à l'Aurélien supérieur. Au contraire, les données paléobotaniques montrent une diminution progressive des espèces arborées depuis le Pliocène moyen jusqu'au début du Pléistocène inférieur et une augmentation des surfaces occupées par les prairies et les steppes. Ces derniers événements sont attestés par l'apparition des espèces hypsodontes parmi les mammifères. La répartition des faunes de mammifères entre les côtes adriatique et tyrrhénienne de l'Italie centrale, pendant le Pléistocène moyen et supérieur, semble ne pas avoir été influencée par des différences climatiques et environnementales. Quand les données sur l'Adriatique sont plus complètes, il est en fait alors possible d'observer une tendance qui est similaire à celles de la Tyrrhénienne. La plupart des mégaherbivores ont une origine asiatique, et on peut émettre l'hypothèse que dans les phases interglaciaires, l'Appennin toscan-émilien a permis aux taxons qui venaient du Nord-Est de l'Europe, de rentrer et se diffuser sur la côte de la mer Tyrrhénienne, plus diversifiée, alors que durant les périodes glaciaires, ils ont suivi l'étroit couloir de la Ligurie. Cette recherche confirme encore le rôle de la péninsule italienne comme aire de refuge de l'Europe continentale; cette condition particulière a permis aux faunes de mammifères italiennes de développer des lignées endémiques (comme *Elephas antiquus italicus* Osborn, 1931, *Cervus elaphus rianensis* Leonardi & Petronio, 1974, *C. e. aretinus* Azzaroli, 1947, etc.). Pour terminer, la biodiversité a subi une forte chute dans les derniers 30 000 ans, très probablement provoquée par les activités anthropiques et le refroidissement climatique du dernier périglaciaire.

MOTS CLÉS

Biochronologie,
Italie,
Pliocène,
Pléistocène,
grands mammifères.

INTRODUCTION

Large mammal diffusion in Italian peninsula since Middle Pliocene to Late Pleistocene are conditioned mainly by the climatic fluctuations, that noticeably changed the ecological niches. These fluctuations seem to have developed a particular role, especially in the second part of the Pleistocene.

Trophic networks changed during this period because of a reduction of vegetation and/or by a gradual formation of different types of vegetation; and even the ecosystems were conditioned by the quantity and the quality of the migration of herbivorous macromammals that are pushed towards the southern regions because of different climatic events. The progressive climatic change

in the Late Pliocene and the Pleistocene towards temporal intervals with lower mean temperatures, which caused forests and woods to thin out and be replaced by open habitats, allowed herbivorous mammals, among which pachyderms, to occupy the territory; these large mammals surviving even under unfavorable climatic conditions. Naturally, a gradual diffusion of cursorial hunters of different sizes successively followed the settlement herbivorous mammals. These carnivores (the ones following the herbivores and pachyderms) will gradually replace those from the Pliocene and the first part of the Pleistocene (Gliozzi *et al.* 1997; Petronio & Sardella 1999; Petronio *et al.* 2007).

The paleobotanical data need to be considered within these global transformations over time. They demonstrate a noticeable latitudinal differentiation of the vegetation that had already begun in the Messinian (Favre *et al.* 2007). In this period open and steppic environments that had continued even through the Pliocene (Suc & Bessais 1990; Suc *et al.* 1995a, b) already existed in southern Italy, while in continental Europe thick forests were present with a temperate climate; one similar to present-day Southern China (Favre *et al.* 2007; Martinetto 1996, 1999). This type of Mio-Pliocene forest extended into much of Central Europe, until Moldavia (Mai 1995), if not all the way into Georgia (Shakryl 1990), and in Italy it impeded and/or slowed down the penetration of prairie mammals that had already existed in Western Europe.

In addition to these climatic oscillations, some effects for the bioevents could have been occurred by the numerous paleomagnetic reversals that occurred in the Pliocene and in the Pleistocene (Sardella *et al.* 1998). According to geophysicists, every one of these reversals takes about 5000 years to complete (Merrill *et al.* 1996). This distresses the biological compass of the animals migrating from Asia or Africa in search of new territories.

According to Gliozzi *et al.* (1997) these faunal changes are grouped in the Mammal Ages and in the Faunal Units. This allows a better understanding of how the dispersal events are connected to environmental and floristic conditions in a highly diversified territory like Italian peninsula.

The floristic characteristics and vegetation changes referable to each Faunal Unit have been reconstructed not only on the basis of the ecophysiological indications of the mammal species, but also on the basis of the flora fossil record (macro- and micropaleobotanical data).

As regards to the peninsula, considering that the Alps and the Po plain are part of continental Europe, the macromammal remains found in the central part of the peninsula, which also better represents the southern part of Europe, have been analyzed. Paleontological data from Puglia and in general from southern Italy have been disregarded since, beyond the relative scarcity of information, the remains of mammal fauna relative to sites in these regions often reveal particular aspects probably attributable to a moderate degree of endemism. The results of these analyses, relative to the fossil remains of Tuscany, Latium, Marche, Umbria, Abruzzo, and Molise have been compared with paleofaunal, biochronological, and paleoenvironmental data of all of the peninsula reviewed after Gliozzi *et al.* (1997).

The aims of this paper are therefore: the identification of the main faunal turnover in Italy; the possible discrepancies between these turnovers and those recorded in the central part of the Italian peninsula; the connection with the climatic variations and/or the Pleistocene changes in the environment – a possible correlation of the dispersal events with magnetostratigraphical changes; and, last, the relationship between several taxa and human activity, especially in the Late Pleistocene.

PRELIMINARY REMARKS ON THE PLIO-PLEISTOCENE BIOCHRONOLOGY

The biochronological study of the vertebrate faunas is based on the biostratigraphical concept of *assemblage zone* sequences (Gliozzi *et al.* 1997). Thus, the fossil remains of animals that *presumably* lived in the environments surrounding the depositional basin have been studied, observing also the paleoecological congruity and the evolutionary degree. This fossil assemblage defines a Local Fauna.

A particular Local Fauna wherein the greatest number of taxa is well represented and wherein one

or more bioevents are pointed out for the first time (First Occurrences) is defined as a Faunal Unit. A few Faunal Units together, with a certain degree of ecological homogeneity, represents a Mammal Age; and this represents a large temporal interval, characterized by the occurrence of particular bioevents on a global scale (Gliozzi *et al.* 1997).

The Local Faunas, the Faunal Units and the Mammal Ages are integrated and correlated, when possible, with radiometric dating, magnetostratigraphical data, and oxygen (marine) isotopic stages (OIS/MIS). These data make it possible to define the temporal interval with sufficient approximation and then to arrange the numerous faunal sequences.

Since the data concerning these faunal assemblages is dependent on the fossil remains known up until today, it is evident that the temporal intervals between one Faunal Unit to the next are destined to vary, and at most, become more and more narrower; precisely because the recognition of either the taxa's initial appearance (F.O.) or the final appearance (L.O.) changes. Inasmuch as it is understandable that the Faunal Units are based on the presence and the migration of mammals in a regional area, most of the biochronological data that concern a specific territory can be difficult to extrapolate in a different region. This methodology, therefore, can only have a good regional utility. To correlate the dispersal events data in Italy with other European regions, references will need to be made to the radiometric chronology and to the relationships with the chronostratigraphy of the marine sediments (e.g., Early, Middle and Late Pleistocene). This feature obviously does not nullify the use of the Faunal Units, which in the field of a determined area can be considered a valid instrument to define the sequences of biochronological bioevents.

Between approximately 3.3 to 0.01 Ma (Middle Pliocene-Holocene), wherein the modern faunas were formed, three Mammal Ages have been defined (Gliozzi *et al.* 1997; Petronio *et al.* 2007):

1. Villafranchian: from ~3.3 to ~1.1 Ma (Middle Pliocene and part of the Early Pleistocene);
2. Galerian: from ~1.1 to ~0.35 Ma (part of the Early Pleistocene-late Middle Pleistocene);
3. Aurelian: from ~0.35 to ~0.01 Ma (late Middle Pleistocene-Late Pleistocene).

In regards to these Mammal Ages some temporal ranges of Faunal Units have been revised, the taxonomy of different species have been updated, and a few Faunal Units have recently been created (Petronio *et al.* 2007). These variations are reported in Figure 1 and in the text that follows.

THE VILLAFRANCHIAN MAMMAL AGE

The Villafranchian has recently been subdivided into early, middle and late (Gliozzi *et al.* 1997) with eight Faunal Units (F.U.):

- Early (~3.3 to 2.6 Ma): Triversa, Montopoli;
- Middle (~2.6 to 1.8 Ma): Saint Vallier, Costa San Giacomo;
- Late (~1.8 to 1.1 Ma): Olivola, Tasso, Farneta, Pirro.

A renewal of the fauna is documented in Italy at the beginning of the Villafranchian, with a clear transition from the Ruscinian and archaic faunas, typical of temperate-warm environments, to faunas with more modern characteristics, indicative to less humid environments under cooler climates.

The age of the first F.U., Triversa, on the basis of paleomagnetic data, has been determined to be around 3.3 Ma (Lindsay *et al.* 1980). The faunas are characterized by the occurrence of new species and by the diffusion of animals also adapted to open habitats: among the carnivores, *Chasmaporthetes lunensis* Del Campana, 1914, *Acinonyx pardinensis* (Croizet & Jobert, 1828), *Homotherium crenatidens* (Weithofer, 1889) and a small bear of modern form, *Ursus minimus* Devèze & Bouillet, 1827 can be considered; amongst the herbivores, *Axis lyra* (Azzaroli, 1992) replaces the small Ruscinian cervids, *Leptobos stenometopon* (Rutimeyer, 1867), which replaced the Ruscinian antelopes, *Stephanorhinus jeanvireti* (Guérin, 1972) and *Mammuth (Zygodolophodon) borsoni* (Hays, 1834). Aside these new species, persisting from the Ruscinian, are *Anancus arvernensis* (Croizet & Jobert, 1828), *Tapirus arvernensis* (Croizet & Jobert, 1828), *Macaca sylvanus* (Linnaeus, 1758) and *Sus minor* (Depéret, 1890). In addition, the paleobotanical data indicate a considerable homogeneity of the vegetation, at least in Northern Italy, to the passage from the Ruscinian to the early Villafranchian; therefore, the survival of the animals strictly reliant on the

forests is not surprising. Nevertheless, specifically in the sediments of the Val Trivera (Martinetto & Mai 1996), like those of the coeval Fossil Forest of the Stura di Lanzo (Martinetto *et al.* 2007), floral elements that clearly indicate the predominance of willow trees in the mesofil forests have been identified, to the detriment of evergreen species that before 3.2 Ma were more abundant, if not predominant (Martinetto 1999).

An important faunal renewal, likely related to global climate cooling at about 2.7-2.5 Ma (MIS 104-100) occurred. This event coincides with an irreversible transformation of the climate regime that determines rapid variations of the vegetation community, according to a repetitive succession of vegetation types (Leroy 2007). The entire interval between 2.5 and 1.0 Ma is characterized by relatively long interglacial periods, with rather thick forestal covering, and short glacial periods, with open vegetation or partly arboreal vegetation in Central and Southern Italy.

On the contrary, in Northern Italy, even the glacial periods were characterized by extensive forestal coverings; predominately microtherm conifers like *Picea* Link (Ravazzi 2002; Monegatti *et al.* 2002). By using the macropaleobotanical data (Mai 1994; Cavallo & Martinetto 2001) it is possible to point out that these conifers did not belong to the current boreo-alpine lineage, but instead to a family of Asiatic origin: *Picea florschuetzii* Van der Hammen.

The disappearance of *Tapirus* Brisson, 1762 and *Mammuth Blumenbach*, 1799, and the appearance of *Equus livenzovensis* Bajgusheva, 1978 and *Mammuthus gromovi* (Alexeeva & Garutt, 1965) signal the passage to the Montopoli F.U., corresponding with the Gauss-Matuyama transition (Lindsay *et al.* 1980; Sardella *et al.* 1998). An abrupt reduction of the forests in favor of taxa adapted to open lands and arid climates, characterizes the transition between the two F.U.'s, defined the Equus-Elephant event (Azzaroli 1977). These taxa came from the East or from the Central-European regions. Even the giant Cervidae Gray, 1821, *Eucladoceros falconeri* Dawkins, 1868, appeared along with *Croizetoceros ramosus* (Croizet & Jobert, 1828), *Gazella borbonica* Depéret, 1884 and *Stephanorhinus etruscus* (Falconer, 1868). Amongst the Carnivores, *Lynx issiodorensis*

(Croizet & Jobert, 1828), *Megantereon cultridens* (Cuvier, 1824) and *Pliocrocuta perrieri* (Croizet & Jobert, 1828) are present.

The paleobotanical data that better illustrate the progressive opening of the vegetation during the cold phases from MIS 108 to MIS 98 are provided by the Garraf 1 (Catalonia, Spain) (Suc & Popescu 2005). The Italian sites, on the other hand, do not provide precise indications on this opening of the vegetation, probably because continuous sections in the Tyrrhenian zone are missing. These sections cover the crucial, initial interval of when the fauna of Montopoli began. Evidence of steppic, open vegetation has been found in the Rena Bianca succession of the Upper Valdarno (Bertini 2006). This vegetation is characterized by the abundance of *Artemisia* L. In the Pliocene succession of San Miniato-Montopoli, from which the mammal fauna comes, the palynological analyses of Bertini (in Benvenuti *et al.* 2007) has shown evidence of the passage from warm-temperate forests to cooler ones. These cooler forests are characterized by the prevalence of conifers like *Picea*, recorded in strata older than that bearing the Montopoli mammal fauna (and for which paleobotanical data are lacking).

The middle Villafranchian is represented mainly in French deposits (in particular Saint Vallier, see for example Guérin *et al.* 2004). In this phase *Equus stenonis* Cocchi, 1867 appears, replacing the large *E. livenzovensis* and *Mammuthus meridionalis* (Nesti, 1824). The latter can be considered as the first, advanced mammoth that lived in open habitats.

Coste San Giacomo F.U. is a slightly more recent unit of Late Pliocene. In Italian peninsula the faunal changes continue with the evolution of proboscideans, perissodactyls and cervids (*Eucladoceros tegulensis* (Dubois, 1904)) and with the arrival of *Leptobos* ex gr. *merlai* De Giulii, 1987 -*furtivus* Duvernois & Guérin, 1988, *Gazellospira torticornis* (Aymard, 1854), *Sus strozzii* Forsyth Major, 1881 and of the carnivore *Canis* ex gr. *C. etruscus* Forsyth Major, 1877.

Paleobotanical data directly associated with mammal faunas are missing from both of the Villafranchian F.U.'s. Nevertheless, the long pollen diagram of Pontini & Bertini (2000) provides extremely important information on the variation of

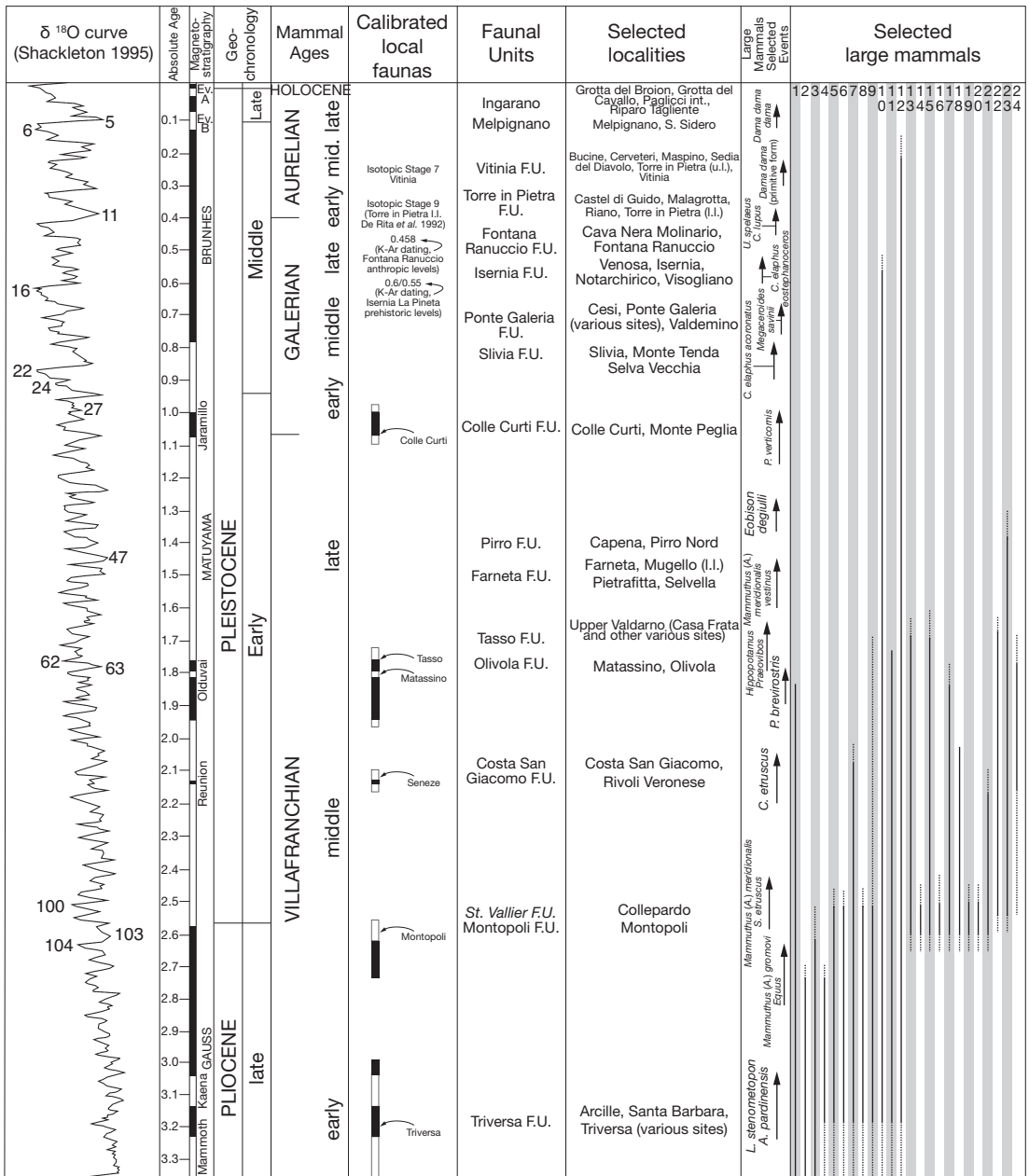
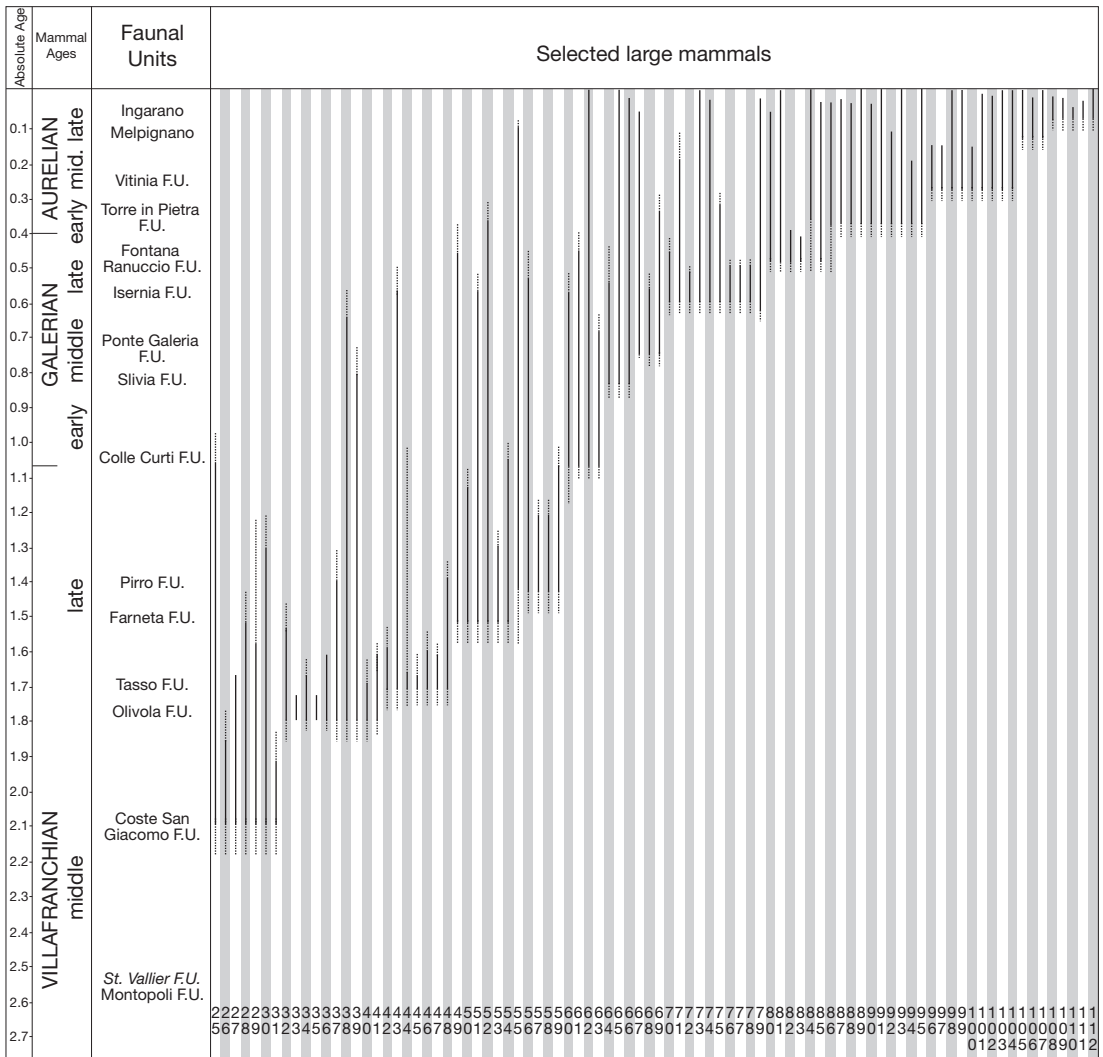


FIG. 1. — Distribution, first occurrences and last occurrences of the main macromammals on the Italian peninsula. Selected large mammals numbers: 1, *Anancus arvernensis*; 2, *Tapirus arvernensis*; 3, *Sus minor*; 4, *Mammuth borsoni*; 5, *Stephanorhinus jeanvireti*; 6, *Leptobos stenometopon*; 7, *Axis lyra*; 8, *Ursus minimus*; 9, *Acinonyx pardinensis*; 10, *Homotherium latidens*; 11, *Chasmaportetes lunensis*; 12, *Lynx ex gr. issiodorensis*; 13, *Megantereon cultridens*; 14, *Mammuthus gromovi*; 15, *Stephanorhinus etruscus*; 16, *Equus livenzovensis*; 17, *Gazella borbonica*; 18, *Nyctereutes megamastoides*; 19, *Croizetoceros ramosus*; 20, *Eucladoceros falconeri*; 21, *Pliocrocota perrieri*; 22, *Mammuthus meridionalis meridionalis*; 23, *Equus stenonis*; 24, *Leptobos merlai-furtivus*; 25, *Macaca sylvanus*; 26, *Gazellospira torticornis*; 27, *Gallogoral meneghini*; 28, *Canis etruscus*; 29, *Sus strozzi*; 30, *Vulpes alo-*



pecoides; **31**, *Eucladoceros tegulensis*; **32**, *Leptobos etruscus*; **33**, *Procampoceros brivatense*; **34**, *Eucladoceros dicranios*; **35**, *Enhydrictis ardea*; **36**, *Axis nestii*; **37**, *Ursus etruscus*; **38**, *Panthera gombaszoegensis*; **39**, *Pachycrocuta brevirostris*; **40**, *Felis lunensis*; **41**, *Canis arnensis*; **42**, *Equus stehlini*; **43**, *Hippopotamus antiquus*; **44**, *Leptobos vallisarni*; **45**, *Eucladoceros ctenoides*; **46**, *Lycyaon falconeri*; **47**, *Pannonictis nestii*; **48**, *Hystrix refossa*; **49**, *Axis eurygonos*; **50**, *Mammuthus meridionalis vestinus*; **51**, *Stephanorhinus hundsheimensis*; **52**, *Equus ex gr. bress.-sussenbornensis*; **53**, *Praemegaceros obscurus*; **54**, *Megantereon whitei*; **55**, *Canis mosbachensis*; **56**, *Equus altidens*; **57**, *Bison degiulii*; **58**, *Theroptheus sp.*; **59**, *Lycyaon lycaonides*; **60**, *Bison schoetensacki*; **61**, *Ursus deningeri*; **62**, *Sus scrofa*; **63**, *Praemegaceros verticornis*; **64**, *Cervus elaphus acoronatus*; **65**, *Capreolus capreolus*; **66**, *Crocota crocuta*; **67**, *Elephas antiquus*; **68**, "Bos" galerianus; **69**, *Mammuthus trogontherii*; **70**, *Praemegaceros solihacus*; **71**, *Stephanorhinus kirchbergensis*; **72**, *Megaloceros savini*; **73**, *Meles meles*; **74**, *Equus ferus*; **75**, *Dama clactoniana*; **76**, *Panthera fossilis*; **77**, *Hyaena prisca*; **78**, *Hemitragus bonali*; **79**, *Panthera pardus*; **80**, *Hippopotamus amphibius*; **81**, *Bos primigenius*; **82**, *Cervus elaphus eostephanoceros*; **83**, *Cuon priscus*; **84**, *Ursus arctos*; **85**, *Stephanorhinus hemitoechus*; **86**, *Bison priscus*; **87**, *Panthera spelaea*; **88**, *Ursus spelaea*; **89**, *Canis lupus*; **90**, *Megaloceros giganteus*; **91**, *Vulpes vulpes*; **92**, *Hystrix vinogradovi*; **93**, *Mustela putorius*; **94**, *Cervus elaphus rianensis*; **95**, *Felis silvestris*; **96**, *Mammuthus chosaricus*; **97**, *Cervus elaphus aretinus*; **98**, *Capra ibex*; **99**, *Rupicapra rupicapra*; **100**, *Dama dama tiberina*; **101**, *Equus hydruntinus*; **102**, *Gulo gulo*; **103**, *Mustela nivalis*; **104**, *Martes martes*; **105**, *Cervus elaphus elaphus*; **106**, *Dama dama dama*; **107**, *Lynx lynx*; **108**, *Cuon alpinus*; **109**, *Mammuthus primigenius*; **110**, *Marmota primigenia*; **111**, *Coelodonta antiquitatis*; **112**, *Mustela erminea*.

the vegetation in Central Italy during part of the Late Pliocene (middle Villafranchian). This diagram shows two long phases, in which the glacial intervals are characterized by open, steppe-type vegetation. During these alternate phases the forests seem to be present in the long interglacial periods and in the short glacial intervals. The sampling resolution of the mammal assemblages is still insufficient to discriminate between one specific type of vegetation to another. However, one can hypothesize that the aforementioned prairie animals, which reached Central Italy in the middle Villafranchian, had an advantage in open lands (generated in the “steppic” phases) and they could have even then caused an impact on the vegetation, preventing its closure when favorable climatic conditions came back.

The passage to the late Villafranchian faunas was achieved at the end of the Pliocene. The Olivola F.U. (its name deriving from the site of Val di Magra) corresponds to the upper part of the Olduvai subchron, dated at about 1.7 Ma. The fauna is characterized by the arrival of Canidae (Fischer de Waldheim, 1817) Gray, 1821, *Canis arvensis* Del Campana, 1913, similar to the jackal, and by *Lycaon falconeri* (Forsyth Major, 1877); thus confirming the reduction of the forests, together with the diffusion of species adapted to steppic or prairie areas, like the medium-large sized bovid *Leptobos etruscus* (Falconer, 1868), together with *Equus stenonis* and *Mammuthus meridionalis*. Forest environments are still present as confirmed by the first occurrence of the Eurasian jaguar (*Panthera gombaszoegensis* (Kretzoi, 1938)), a bear (*Ursus etruscus* Cuvier, 1823) and two new species of Cervidae (*Eucladoceros dicranios* (Nesti, 1841) and *Axis nestii* (Azzaroli, 1947)). *Pliocrocota perrieri*, *Anancus arvernensis* and *Gazella borbonica* disappeared.

Direct paleofloristic evidence is available for the sites of Torre Picchio and Villa San Faustino (Girotti *et al.* 2003), where a temperate-warm vegetation of willow forest and a mixed forest of conifer-willow (with a temperate-cold climate) has been documented. The presence of *Picea* macrofossils at low altitudes testifies the harshness of the climate even in Central Italy. The reduction of the forest, indicated by the mammals, is confirmed also by the already cited steppic phase, shown in the upper part of the

pollen diagram of Pontini & Bertini (2000) or in successive phases.

In regards to the F.U. immediately following (Tasso), a palynological study in the Poggio Rosso (Upper Valdarno) area has recently been conducted, which has pointed out forestal phases that are spaced-out by herbaceous phases, indicating open lands, precisely corresponding with a deposit rich in vertebrates (Mazza *et al.* 2004). Nonetheless, forest phases are well documented in the same area, even by macrofossils of trees with an Asiatic (*Cephalotaxus* Siebold & Zuccarini, *Pterocarya* Kunth), American (*Juglans bergomensis* (Balsamo-Crivelli)) or Asiatic-American (*Liquidambar* Linnaeus, *Liriodendron* Linnaeus) affinity (Martinetto 2001). In general, even the mammals of this F.U. seem to indicate the predominance of open lands that will be accentuated in the following F.U.'s, with the arrival of new species typical of steppe/prairie environments.

The large-sized canid *Lycaon falconeri* appears. Moreover a medium-sized equid, *Equus stehlini* Azzaroli, 1965, adapted to running, and a leptobovine, with a morphology similar to a bison *Leptobos vallisarni* Merla, 1949 also occur. Other Bovidae of medium size, however, disappear. The genus *Eucladoceros* Falconer, 1868 is present with two new species: *E. dicranios* and *E. ctenoides* (Nesti, 1841).

In addition the large-sized hippopotamus (*Hippopotamus antiquus* Desmarest, 1822), much adapted to aquatic life, has been recorded at Monte Riccio (associated with a late Villafranchian fauna) (Mazzini *et al.* 2000). The Upper Valdarno specimen have to be referred, according to Napoleone *et al.* (2003), to a depositional cycle younger than that bearing the Tasso F.U. mammal assemblages (possibly to be referred to Farneta F.U.).

During the Early Pleistocene a more marked renewal of the faunas took place, with a progressive disappearance of the Villafranchian species and the gradual arrival of new species that will characterize the Middle Pleistocene. In the Farneta F.U., alongside the large Villafranchian Cervidae and Bovidae Gray, 1821 of the genus *Leptobos* Rüttimeyer, 1877 and *Eucladoceros* comes a primitive form of giant megacerine deer (*Praemegaceros*

obscurus (Azzaroli, 1953)); megacerine deers will dominate the assemblage in the Galerian, substituting the genus *Eucladoceros*. The evolution among the medium-sized Cervidae continues in loco with the genus *Axis* Gray, 1825: *Axis nestii* is substituted by a more advanced form (*Axis eurygonos* (Azzaroli, 1947)) with antlers and pedicle clearly shorter, and with the first beam in proximity to the rose with a more obtuse angle (Di Stefano & Petronio 2002). Among the Perissodactyla, the equid *Equus sussenbornensis* Wüst, 1901 and a small-sized rhino, *Stephanorhinus* cf. *hundsheimensis* (Toula, 1902), are present. *Mammuthus meridionalis* is present with an advanced form referred, in the past century, to *M. m. vestinus* Azzaroli, 1977. Recent analyses of the Early Pleistocene elephantids from Italy suggest that this form could be considered not valid, and differences in the specimens due to intraspecific and ontogenetic variability (Palombo & Ferretti 2005). From a paleobotanical point of view the aforementioned faunal renewal cannot easily be explained because the long pollen diagram available for the Pietrafitta site (Lona & Bertoldi 1973) does not show evidence of drastic changes of the vegetational successions and of the cyclicity in respect to the preceding intervals.

In the successive Pirro F.U., the data indicate the prevalence of open lands. In fact a primitive bison, *Bison degiulii* (Masini, 1988), which indicates more rigid and arid conditions that are not fit for the leptobovine, and a light built, medium-sized Equidae, *Equus altidens* Reichenau, 1915, occur for the first time. The large-sized and robust *E. sussenbornensis* is still present. *Lycaon lycaonoides* (Kretzoi, 1938), *Hystrix refossa* Gervais, 1852, and Cercopithecidae Gray, 1821 of African origin, *Theropithecus* Geoffroy, 1843 (Rook *et al.* 2004; Rook & Sardella 2005) appear. During this temporal interval (1.3–1.6 Ma) in the quarries of Pirro Nord, the most ancient evidence of humans in Europe, testified by lithic artefacts, were found (Arzarello *et al.* 2007).

THE GALERIAN MAMMAL AGE

The transition between the typical Villafranchian faunas and the Galerian ones (more modern and without Pliocene taxa) was a gradual phenomenon that lasted over a span of about 500 000 years.

During this period, new species, typical of steppic/prairie environments, reached in Italy from the east and from Central Europe joining the Villafranchian species that progressively disappeared.

The appearance of *Praemegaceros verticornis* (Dawkins, 1872) has been chosen as the bioevent that marks the beginning of the Galerian Mammal Age (Gliozzi *et al.* 1997). This species is a large sized cervid that was reported for the first time in the Colle Curti (Marche) local fauna, which has also been correlated to the base of the Jaramillo subchronus (about 1.1 Ma). This moment, well-known through the marine isotopic record and through continental pollen diagrams, represents another important point of radical transformation of the climatic and vegetational cycles (“mid-Pleistocene revolution”). In fact, the passage to a phase characterized by long glaciations is observed with 100 000 years cycles. The difference between the temperatures during glacial and interglacial phases becomes more pronounced (Leroy 2007). In northern Italy, the macro- and microfloristic findings of Ranica (Ravazzi *et al.* 2005) demonstrated that, during the glacial phase corresponding to the Jaramillo subchron (MIS 30), the flora was already represented by species that are still living in the present day (e.g., *Larix decidua* Miller and *Picea abies* (Linnaeus)). In the Ranica site a cold, steppic phase is well documented in which an Alcin was found (*Cervalces latifrons* (Johnson, 1874)); nevertheless, an arboreal covering remains present at the foot of the Alps even during this phase. On the contrary, in Central Italy, the pollen diagrams of Colle Curti and Cesi (Bertini 2000) show high percentages of herbaceous forms, a clear evidence of more open vegetation. Furthermore, this vegetation was replaced by arboreal vegetation during short temporal intervals. The fauna of early Galerian is relatively scarce, but it has innovative elements, especially among the micromammals (Kotsakis *et al.* 2003). Many Villafranchian species still persist: *Pachycrocuta brevirostris* Aymard, 1846, *Panthera gombaszoegensis* and *Homotherium* Fabrini, 1890 among the carnivores; *Stephanorhinus* cf. *hundsheimensis* and *Hippopotamus antiquus* among the herbivores.

Three F.U.’s are recognizable within the middle Galerian faunas on the basis of the percentage of

leftover (Villafranchian) forms and the percentage of new forms (that entered or locally differentiated). During this temporal interval the most remarkable and documented faunal renewal occurred. In the Slivia F.U., dated about 850 000 years ago, *Axis eurygonis* is still present and several first occurrences are recognizable: *Cervus elaphus acoronatus* (Beninde, 1937) (an archaic subspecies of the red deer), *Sus scrofa priscus* Goldfuss, 1832 (the first wild boar), *Bison* cf. *schoetensacki* Freudenberg, 1910 (an archaic form of bison), *Stephanorhinus hundsheimensis* (a small-sized rhino of open lands), more advanced forms of *Mammuthus* (M. cf. *tamanensis* (Dubrovo, 1964), M. cf. *trogontherii* Brookes, 1828), the first archaic form of *Elephas* (E. cf. *antiquus* Falconer & Cautley, 1847), *Crocota crocuta* Erxleben, 1777 (the spotted hyena) and *Ursus deningeri* Linnaeus, 1758. *Pachycrocota* Kretzoi, 1938 and *Megantereon* Croizet & Jobert, 1828 disappear.

In the slightly more recent Ponte Galeria F.U. (about 750 000 years ago) (Petronio & Sardella 1999), *Bos galerianus* Petronio & Sardella, 1998, a bubaline bovid, has its first occurrence and, among the megacerini there is *Megaloceros savini* Brookes, 1828. *Elephas antiquus*, which will survive until the last glacial, and *Mammuthus trogontherii* both spread out.

The Isernia F.U., dated at around 550-600 000 years ago (Coltorti *et al.* 2005), is characterized by the first occurrence of *Panthera fossilis* (Reichenau, 1906) (a primitive lion), by *Equus ferus* Linnaeus, 1758 (= *Equus caballus*, Gliozzi *et al.* 1997), by several Caprinae (*Hemitragus* Hodgson, 1841 and *Ovis antiqua* Linnaeus, 1758), by another large-sized Cervidae (*Praemegaceros solilhachus* (Robert, 1829)), by an archaic fallow deer (*Dama clactoniana* (Falconer, 1868)) and by a massive form of rhino (*Stephanorhinus kirchbergensis* (Jäger, 1839)) (Bilia & Petronio 2009). This F.U. is also characterized by the dispersal of *Bison schoetensacki*.

During the late Galerian (Fontana Ranuccio F.U., 460 000-350 000 years ago) the faunal renewal is completed. The last Villafranchian species disappear (except possibly *Homotherium*) and numerous species appear: *Cervus elaphus eastephanoceros* Di Stefano & Petronio, 1993 (a more advanced form of red deer characterized by a slight hint of

a crown), *Ursus arctos* Linnaeus, 1758 (the brown bear), *Hippopotamus amphibius* Linnaeus, 1758, similar to the recent *Hippopotamus* (Petronio 1995) and less adapted to the aquatic life respect to *Hippopotamus antiquus*, *Bos primigenius* Bojanus, 1827 (the auroch). Considering the rhinos, a prairie form (*Stephanorhinus hemitoechus* (Falconer, 1868)) spreads out and the forestal form (*Stephanorhinus kirchbergensis*) is still present.

THE AURELIAN MAMMAL AGE

The beginning of the Aurelian Mammal Age, can be placed approximately in correspondence of MIS 10. This Mammal Age sees the appearance of the taxa that represent the core of the present day mammal fauna. Changes involve forms typical of all environments: forest, open lands and intermediate environments. The mammal communities become more and more similar to the modern ones, with the diminishing of large-sized forms and the increase of medium and small-sized ones.

The characteristics of the vegetation in Central Italy have been very well documented by long pollen diagrams (Follieri *et al.* 1988) and by the findings of macrofossils concentrated in some interglacial deposits. On the outskirts of Rome the interval is characterized by predominantly open vegetations with relatively brief forestal phases (Roma I, Roma II, Roma III, Eemian and St. Germani I), which only correspond to 1/10 of the time.

In the early Aurelian, the Torre in Pietra F.U. (about MIS 10-8), the modern wolf, *Canis lupus* Linnaeus, 1758, the cave bear, *Ursus spelaeus* Rosenmüller & Heinroth, 1794, the giant deer, *Megaloceros giganteus* Blumenbach, 1799 and the cave lion (*Panthera spelaea* (Goldfuss, 1810)) appear for the first time. Together with these species, different local subspecies of *Cervus elaphus* are present; they show endemic features, witnessed by the particular archaic structure of the antlers. In the deposits referable to this period *Elephas antiquus* and *Bos primigenius* are constantly present; they are the most abundant species, followed by rhinos, horses, deer, hippos and scarce carnivores; and in some sites even the presence of cold avifauna was found.

In the assemblages of the middle Aurelian, referable to the Vitinia F.U., an archaic subspecies

of the modern fallow deer, *Dama dama tiberina* Di Stefano & Petronio, 1997, and a small-sized Equidae with slim limbs, *Equus hydruntinus* Regalia, 1904, appear. Different climatic conditions characterized the peninsula: the mild climate of the Tyrrhenian mountainside allowed the diffusion of *Macaca sylvanus*, while the more arid conditions of the Adriatic side enabled the ibex (*Capra ibex* Linnaeus, 1758) and chamois (*Rupicapra rupicapra* Linnaeus, 1758) to reach the south part of Apulia and with the climate cooling down, mammoths of the *Mammuthus chosaricus* group spread out.

The late Aurelian is characterized by a series of important climatic events that influenced the faunal composition, with the latitudinal migrations and the reduction of the area of many species. In Italy, the faunal assemblages of this period are difficult to define due to local microclimatic factors, which seem to assume a particular importance with the last glacial drawing near.

In the first part of the late Aurelian (MIS 5) many taxa found in the preceding Faunal Units are still present: among the pachyderms there were *Elephas antiquus*, *Mammuthus chosaricus* Dubrovo, 1966, *Stephanorhinus hemitoechus* and, rarely, *Stephanorhinus kirchbergensis* and *Hippopotamus amphibius*. Very common in mountain environments *Capra ibex*, *Rupicapra rupicapra*, and *Marmota marmota* (Linnaeus, 1758) are present, which are associated to many Felidae Gray, 1821 and a large-sized wolf. *Bos primigenius* and *Equus ferus* are very abundant, and less frequent is *Equus hydruntinus*. Amongst the Artiodactyla some changes can be recorded in Cervidae: during the MIS 5, the red deer is present for the first time with the subspecies *Cervus elaphus elaphus*, and the fallow deer (*Dama dama dama* (Linnaeus, 1758)), derived from *Dama dama tiberina*, appears (Di Stefano & Petronio 2000; Petronio *et al.* 2007).

The first occurrence of these Cervidae, together with a rich mammal fauna of temperate-warm climate, allowed the new F.U. of Melpignano (Apulia) to be instituted and a probable temporal interval between 0.120 Ma and 0.070 Ma to be set for this Unit (Petronio *et al.* 2007).

The first occurrence of *Coelodonta antiquitatis* (Blumenbach, 1799), *Mammuthus primigenius*

(Blumenbach, 1799) and of *Marmota primigenia* (Kaup, 1839) seem to be the bioevents that can define a successive temporal interval that goes from MIS 4 (the first sign in Italy of these “cold” mammals) to MIS 3, in which almost all the large pachyderms gradually disappear from the peninsula (Petronio *et al.* 2007). The first presence of *Coelodonta antiquitatis*, together with *Stephanorhinus hemitoechus*, *Elephas antiquus*, *Cervus elaphus elaphus*, *Dama dama dama*, *Equus hydruntinus*, *Vulpes vulpes* (Linnaeus, 1758) and other carnivores such as *Ursus arctos* and *Gulo gulo* (Linnaeus, 1758) and birds like *Nyctea scandiaca* (Linnaeus, 1758), enabled the Faunal Unit of Ingarano to be defined (the last F.U. of the Aurelian Mammal Age) and a probable temporal interval between 0.070 Ma and 0.035 Ma to be set for this unit.

In this chronological interval first *Hippopotamus amphibius* and *Elephas antiquus* disappear, followed later by *Stephanorhinus hemitoechus*. Equidae become abundant with ibex and chamois, which expand their territory, while the fallow deer and the wild boar survive in the southern regions of the peninsula (Petronio *et al.* 2007). Some “cold taxa”, of which are *Pinguinus impennis* (Linnaeus, 1758), *Myotis dasycneme* (Boie, 1825), *Sicista betulina* (Pallas, 1779), *Mustela erminea* Linnaeus, 1758, *Alces alces* (Linnaeus, 1758) and *Rangifer tarandus* (Linnaeus, 1758), make their appearance (Capasso Barbato *et al.* 1991).

With the last pleniglacial (MIS 2) almost all the large mammals progressively disappear. During the maximum ice expansion the last occurrences of *Dama dama dama*, *Crocota crocota*, *Panthera pardus* Linnaeus, 1758 and *Ursus spelaeus* are recorded. In the late glacial, *Megaloceros giganteus*, *Bison priscus* (Bojanus, 1827) also disappear along with almost all the “cold” mammals (in the Alps, however, the white hare and the ermine still exist today). *Lutra lutra* (Linnaeus, 1758) and *Martes foina* (Erxleben, 1777) probably enter in the peninsula only at the beginning of the Holocene (Sommer & Benecke 2004; Petronio *et al.* 2007) while the last occurrences in Italy of the elk (Sala pers. com.), the cave lion and wild Equidae are recorded (Petronio *et al.* 2005, 2007).

ANALYSIS AND COMPARISON OF THE BIOCHRONOLOGICAL DATA FROM CENTRAL ITALY WITH DATA FROM THE WHOLE PENINSULA

PREMISE

Before the analysis of the data concerning the central part of the Italian peninsula, it is worth discussing some methodological issues that will support the analytical results.

The values corresponding to the Mammal Ages from the Villafranchian to the Aurelian are quite similar to the values of the entire Italian peninsula. In an analysis of great detail, instead, considering the single Faunal Units during the three million years, sometimes data from Central Italy is missing. This is only pertinent to the Pliocene and the earliest part of the Pleistocene; for the Middle and Late Pleistocene (an exception being made for the Slivia F.U., which in Central Italy is not represented in any fossiliferous site), the abundance of data enabled the deposits of the whole Italian territory (excluding the islands) to be compared. In this case, the paleobiological survey of the entire Peninsula is similar to that of the central part.

Considering that – from the Galerian to the Aurelian (during the last one million years) – the structural uplift of the Apennines enabled a watershed line to be identified, potential environmental differences between the Tyrrhenian and Adriatic regions have tried to be distinguished.

In this analysis, the macromammals were taken into account because the data concerning micromammals, birds and, sometimes, reptiles are particularly scarce in the Pliocene and in the earliest Pleistocene. As a matter of fact in the Middle Pleistocene and, especially, in the Late Pleistocene, data on micromammals become abundant, and they reflect the environmental changes very well; nevertheless, the same kind of environmental variations can be pointed out by herbivorous macromammals that are very abundant during the entire temporal interval; therefore, correlating only this group of animals to the floristic variation of the peninsula was preferred. In future papers data concerning micromammals will be able to be examined and it will be interesting to compare those analyses with the data of macromammals; this

kind of comparison was already carried out on the most recent phases of the late Villafranchian (Farneta and Pirro F.U.'s) (Kotsakis *et al.* 2008).

These same macromammals were divided into large herbivorous pachyderm, herbivores and carnivores. All the carnivores were taken into account as a single group. During the Late Pliocene and Early Pleistocene, remains of the large-sized carnivores, characterized by ambush and run hunting systems, are present. Instead, during the Middle Pleistocene and, in particular, the Late Pleistocene, medium- and small-sized carnivores seem to prevail.

DISCUSSION

All the following statistical analyses are obtained from Tables 1-6 (see Appendices) relative to the faunal assemblages found in several sites of Central Italy, and they are assigned to the Faunal Units from the early Villafranchian to the late Aurelian. All data are extracted from: Fabiani (1922), Graziosi (1928, 1944), Del Campana (1954), Radmilli *et al.* (1955), Segre & Ascenzi (1956), Acanfora (1962), Grifoni & Radmilli (1964), Cremonesi (1968), Tozzi (1970, 1974), Pitti & Tozzi (1971), Cassoli (1976), Pitti *et al.* (1976), Radmilli (1977), Caloi *et al.* (1979, 1980, 1989), Giustizia (1979), Bianucci (1980), Palmarelli & Palombo (1981), Capasso Barbato *et al.* (1982, 1998), Radi (1982), Bietti (1984), Bulgarelli & Tagliacozzo (1984), Cazzella & Moscoloni (1984), Segre *et al.* (1984), Segre Naldini (1984), Vitagliano (1984), Caloi & Palombo (1987), Alhaique *et al.* (1988, 1998), Wilkens (1991), Bologna *et al.* (1994), Castelletti *et al.* (1994), Ruffo (1995), Alhaique (1996), Boscato (1996), Cerilli & Brocato (1998), Cilli *et al.* (1998), Rustioni *et al.* (1999), Boscato *et al.* (2001), Di Canzio & Petronio (2001), Palombo *et al.* (2002), Petronio *et al.* (2002), Di Canzio *et al.* (2003), Arzarello *et al.* (2004), Guerreschi *et al.* (2005).

In the first diagram (Fig. 2A) the quantity of taxa is influenced by the number of the studied sites; in particular, the minimum values for the taxa relative to the early Villafranchian and to the early and late Galerian are due to the low number of sites found in Central Italy. The MIS 2 is an exception, in which a minimum value for the number of taxa corresponds to a higher number of sites; this ex-

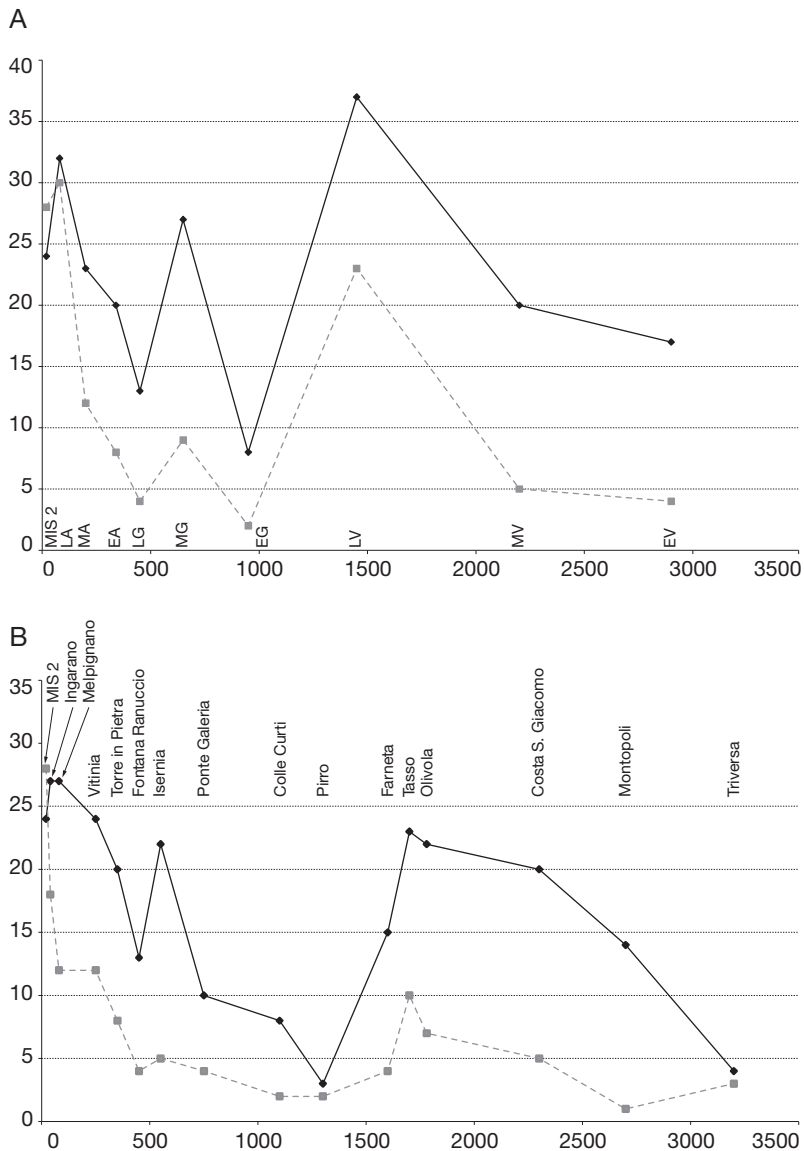


Fig. 2. — **A**, frequency curves of the taxa found in the Mammal Ages of Central Italy (continuous line); quantity of the fossiliferous sites (dashed line); **B**, frequency curves of the taxa found in the Faunal Units of Central Italy (continuous line); quantity of the fossiliferous sites (dashed line). Abbreviations: **MIS 2**, Marine Isotopic Stage 2; **LA**, late Aurelian; **MA**, middle Aurelian; **EA**, early Aurelian; **LG**, late Galerian; **MG**, middle Galerian; **EG**, early Galerian; **LV**, late Villafranchian; **MV**, middle Villafranchian; **EV**, early Villafranchian. In abscissa, time in Ma; in ordinate, number of taxa.

ceptional situation is due to the disappearance of the pachyderms and of the large-sized herbivores, but it is compensated by a high number of studied sites in the final part of the Late Pleistocene.

The same trend, in a more detailed way because it is referred to the F.U.'s, is recognizable in the second diagram (Fig. 2B): the number of species existing in the different temporal intervals is highly elevated es-

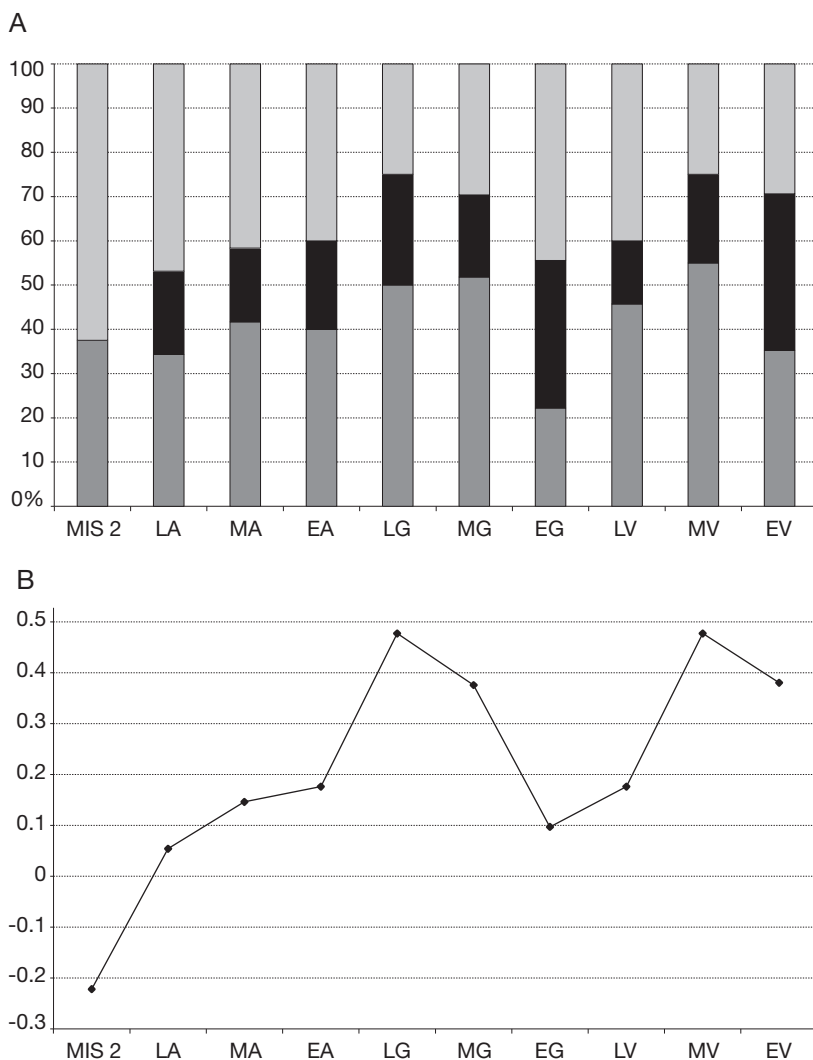


FIG. 3. — **A**, frequency histograms of the quantity of herbivorous taxa (darkgrey), pachyderms (black) and carnivores (lightgrey) living in the Mammal Ages of Central Italy; **B**, medium and large-sized herbivores and carnivores ratio (on logarithmic scale) for Central Italy. Abbreviations: **LA**, late Aurelian; **MA**, middle Aurelian; **EA**, early Aurelian; **LG**, late Galerian; **MG**, middle Galerian; **EG**, early Galerian; **LV**, late Villafranchian; **MV**, middle Villafranchian; **EV**, early Villafranchian; **MIS 2**, Marine Isotopic Stage 2.

pecially in the first part of the late Villafranchian; it is low for the Pirro and Colle Curti F.U.'s, and it increases during the Galerian and the Aurelian, even because it increases parallel to the number of sites taken into account. On the whole, the biodiversity increases from the early Villafranchian to the late Aurelian.

A different statistical analysis was carried out (Fig. 3A) (always in the long temporal interval

comprised between the Middle Pliocene and MIS 2), grouping the herbivorous taxa (bottom), the pachyderms (middle) and the carnivores (top).

The medium and small-sized herbivores (at the bottom) account for about 50% of all the taxa, excluding the minimum value of the early Galerian due to the presence in the territory of Central Italy of only two mammal sites (Colle Curti and

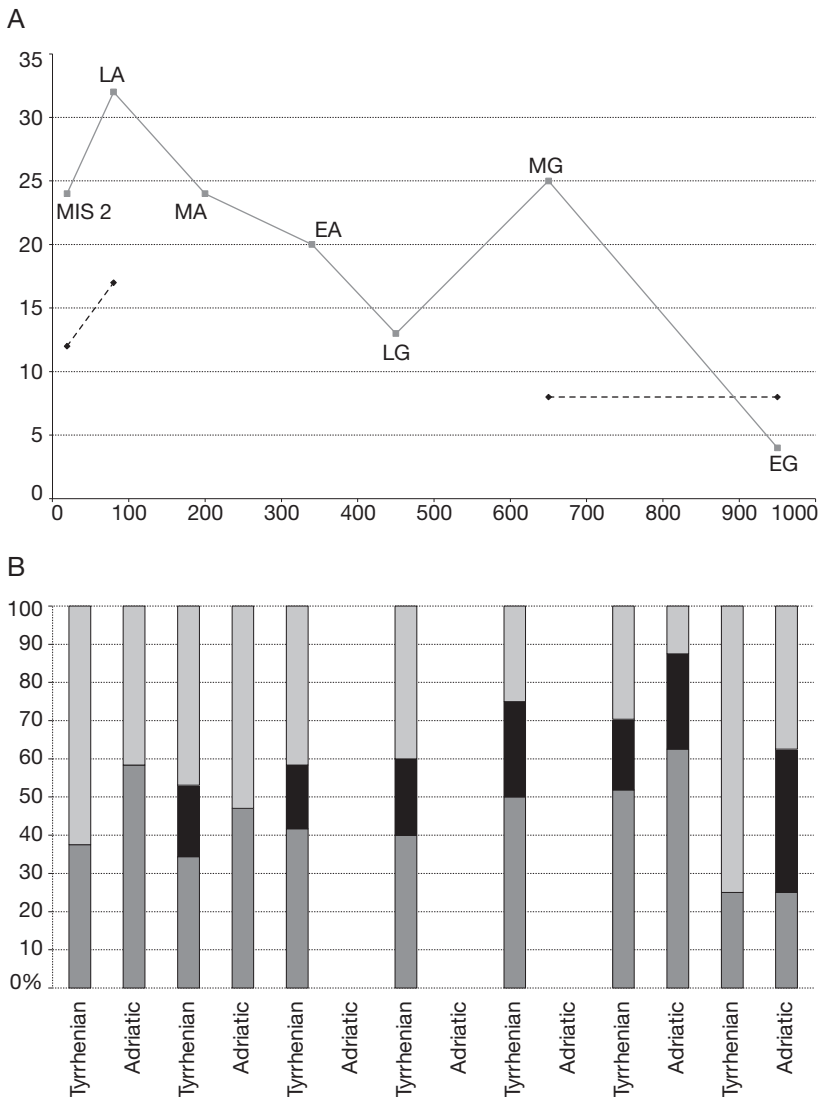


FIG. 4. — **A**, frequency curves of the taxa found in the Mammal Ages of the Tyrrhenian side (continuous line) and of the Adriatic side (dashed line) in Central Italy; in abscissa the time in thousands years, in ordinate the number of taxa; **B**, frequency histograms of the quantity of herbivorous taxa (darkgrey), pachyderms (black) and carnivores (lightgrey) living in the Tyrrhenian and Adriatic side of Central Italy. Abbreviations : **LA**, late Aurelian; **MA**, middle Aurelian; **EA**, early Aurelian; **LG**, late Galerian; **MG**, middle Galerian; **EG**, early Galerian; **MIS 2**, Marine Isotopic Stage 2.

Monte Peglia); as in Gliozzi *et al.* (1997), the site of Monte Peglia is considered to belong to the Colle Curti F.U. because the micromammals show characters compatible with this temporal interval, even if the macromammals are certainly not classifiable.

Pachyderms, after an abundance of many forms in the early and middle Villafranchian, present themselves in quite abundant percentages to the late Aurelian, and then they disappear completely with the last glacial episode. Even in this case, the analysis of the only available site (Colle Curti)

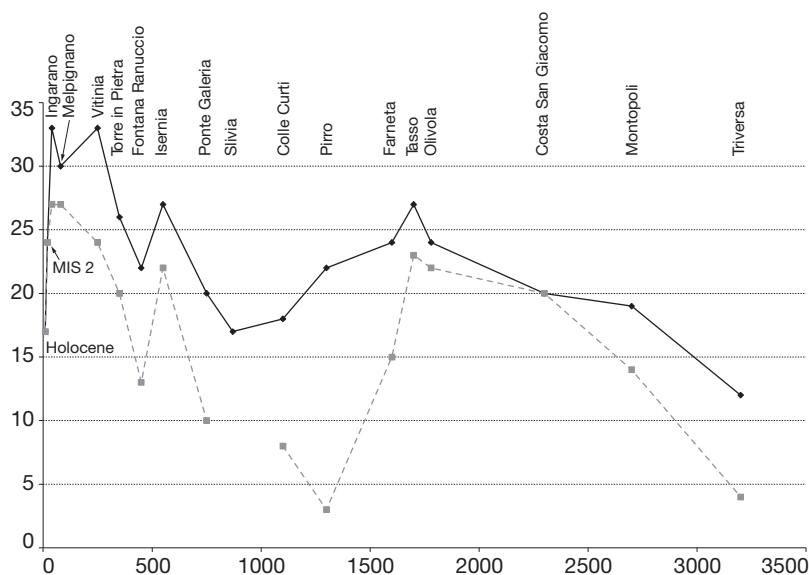


Fig. 5. — Frequency curve of the quantity of species comprised in the temporal interval of the Faunal Units for Italy (continuous line) and for Central Italy (dashed line); in abscissa the time in thousands years, in ordinate the number of taxa. Abbreviations: **MIS 2**, Marine Isotopic Stage 2.

alters the percentage of the occurrences in this temporal interval.

The histograms (UP) indicating the percentage of carnivorous mammals seem to have a peculiar trend: their diversity seems to be low in the first part of the Villafranchian, whereas it increases from the late Galerian to the late Aurelian. The abundance of the carnivorous mammals during the late Villafranchian and of the Galerian is probably due to the presence of medium- and large-sized carnivores characterized by an ambush hunt-way and to the presence of large-sized predator runners. The large number of Mustelidae and other small predators in the Aurelian changes the percentages to the advantage of the carnivores during the last 300 000 years. Nevertheless, it cannot be excluded that this trend is somehow altered by the different number of findings, which is relatively low in the early and middle Villafranchian and in the early Aurelian, whereas it is relatively high and it is contemporaneous to the human presence during and after the late Aurelian.

The following diagram (Fig. 3B) (the x axis shows the herbivores/carnivores ratio; the y axis shows the Mammal Ages; the percentages are expressed on

logarithmic base) points out the same phenomenon: the herbivores/carnivores ratio tends to decrease constantly to the advantage of the carnivores during the last part of the Pleistocene for the same reasons we explained before.

Taking into account the Middle Pleistocene fossiliferous localities of the Tyrrhenian and Adriatic sides (Fig. 4A), it can be observed that the number of taxa from the Tyrrhenian side (continuous line) basically corresponds to the same curve that is found in Central Italy for the same temporal interval. Data from the Adriatic side (dashed line) are, instead, very incomplete for the Galerian and show the same trend on the Tyrrhenian side during the second part of the Aurelian.

Even for the Galerian, taxa were, once again, grouped into herbivores, pachyderms and carnivores. Results of the findings on the two sides are shown in Figure 4B: we can only compare the last 200 000 years because in the central part of the diagram, data from the Adriatic side, are lacking; in the last one million year the relative increase of the small and medium-sized carnivores from the Galerian to MIS 2 is more evident.

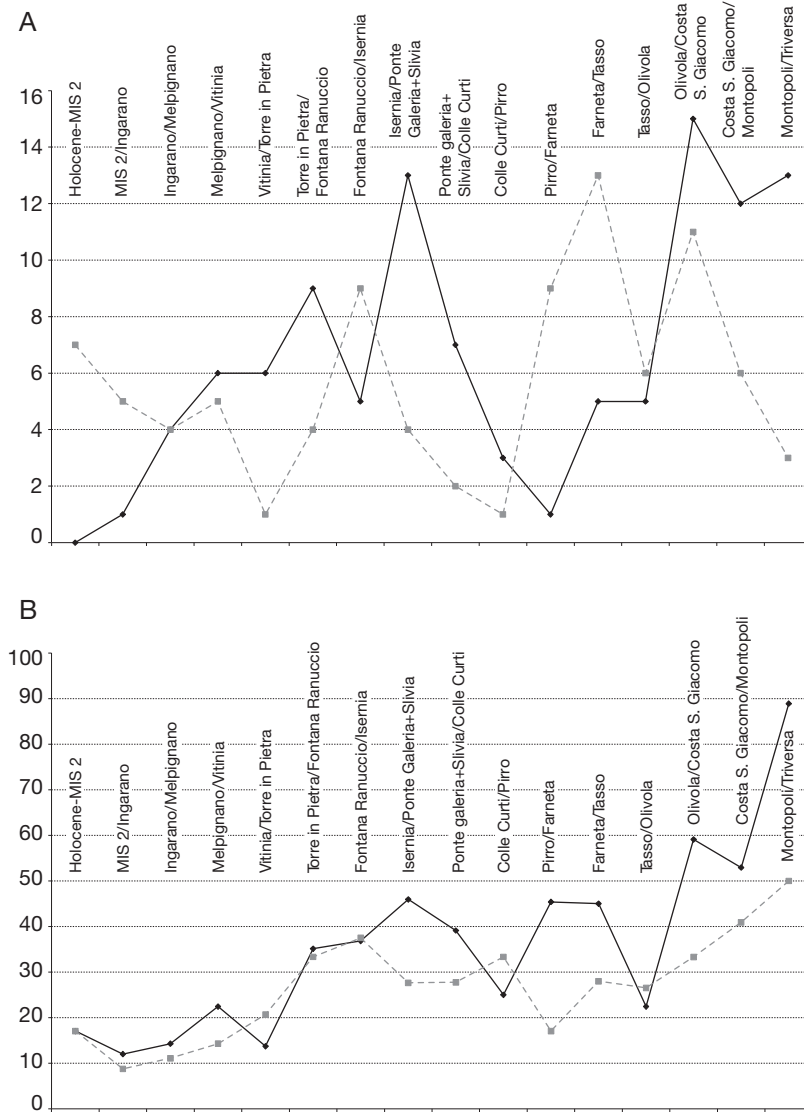


FIG. 6. — **A**, frequency curve of the quantity of First Occurrences (continuous line) and Last Occurrences (dashed line) comprised in the temporal intervals of the Faunal Units for Central Italy (in ordinate the number of taxa); **B**, comparison between the trend of the turnover curves calculated for Italy (dashed) and for Central Italy (continuous line) (in ordinate the values of the turnover index). Ab-abbreviation: **MIS 2**, Marine Isotopic Stage 2.

In Figure 5 the curve corresponding to the number of taxa from Central Italy (dashed line) and the curve corresponding to the number of taxa from the entire peninsula (continuous line) in the distinct Faunal Units are compared (adding the three new Faunal Units not yet mentioned in Gliozzi *et al.* 1997: Ponte Galeria

[Petronio & Sardella 1999]; Melpignano and Ingarano F.U.'s [Petronio *et al.* 2007]). The trend seems quite similar to the F.U. of Isernia to the Aurelian (MIS 2), whereas it diverges from the total curve in the Early Pleistocene (Faunal Unit of Slivia) and in the Pliocene, because of the missing data.

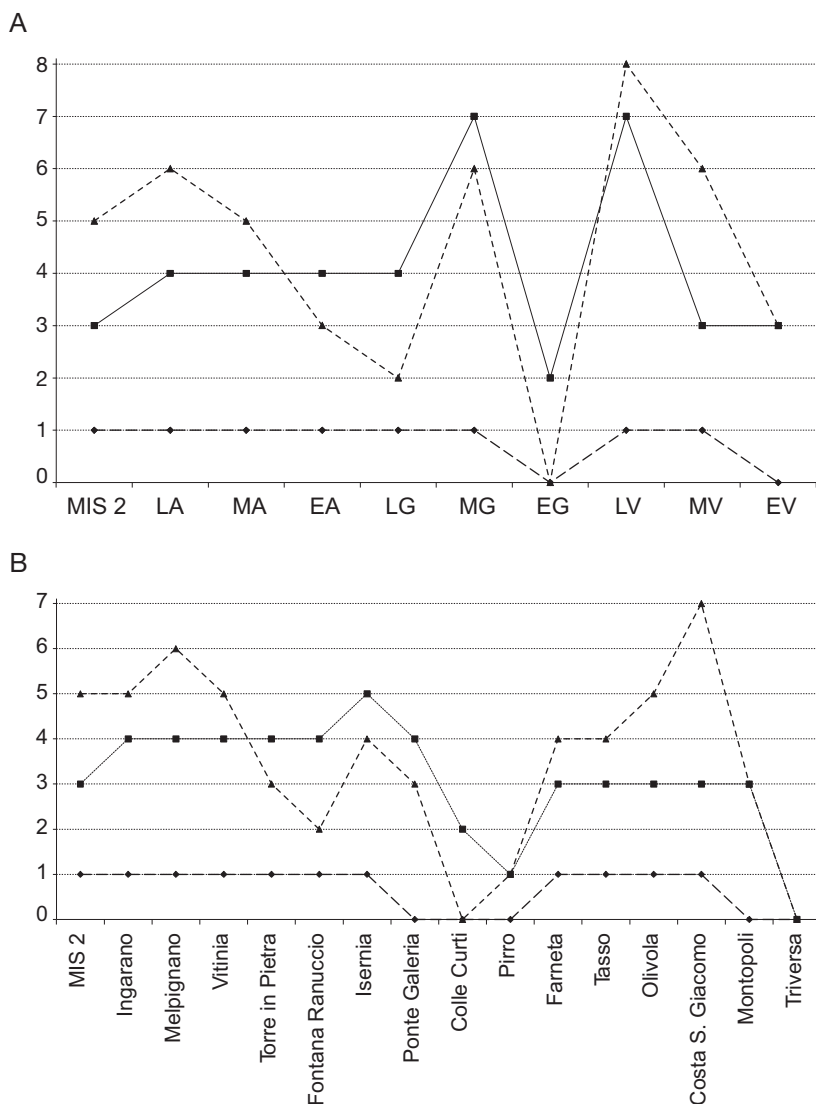


FIG. 7. — **A**, frequency histogram of the quantity of herbivorous brachydonts, mesodonts and hypsodonts for the Mammal Ages of Central Italy; **B**, frequency histogram of the quantity of herbivorous brachydonts, mesodonts and hypsodonts for each Faunal Unit of Central Italy. Abbreviations: **MIS 2**, Marine Isotope Stage 2; **LA**, late Aurelian; **MA**, middle Aurelian; **EA**, early Aurelian; **LG**, late Galerian; **MG**, middle Galerian; **EG**, early Galerian; **LV**, late Villafranchian; **MV**, middle Villafranchian; **EV**, early Villafranchian. In ordinate the number of taxa.

The following Figure 6A shows the trend of the taxa alternating in Central Italy: the continuous line represents the number of first occurrences (FO) of macromammal taxa and the dashed line represents the quantity of last occurring taxa (LO)

at the passage between the Faunal Units; the number of taxa is expressed on the x axis.

The Turnover Indexes (formulas $TI = \%fo + \%lo/2$; $\%fo = fo/Rm \cdot 100$; $Rm = N - (fo + lo/2)$) of the numerous taxa for the entire peninsula (dashed line)

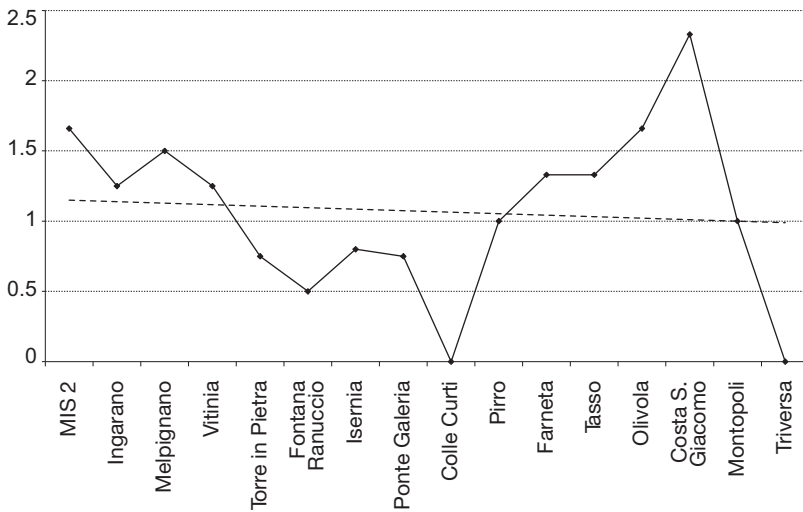


Fig. 8. — Hypsodonts and mesodonts ratio in the Faunal Units showing the tendency line (dashed line). In ordinate the values of the ratio between hypsodont and mesodont taxa. Abbreviation: **MIS 2**, Marine Isotope Stage 2.

and for Central Italy (continuous line) are compared in the following diagram (Fig. 6B; Table 7) through the entire temporal frame reflected in this paper; if the curve that represents the whole peninsula is compared to the one obtained in Sardella *et al.* (1998), slight differences can be noticed, due to how much the data (those relative to the sites and the taxa) have been modified, which has been brought on during the last ten years. The turnover curve, in the temporal intervals referable to Central Italy, diverges from the general one especially in the part related to the early and middle Villafranchian. In fact, this curve shows prevalently higher values (see also Fig. 6A) because, considering the low number of fossiliferous sites, a higher number of first occurring taxa and a lower number of last occurring taxa is found.

Taxa were divided into brachydonts (Suidae), mesodonts (Cervidae) and hypsodonts (Equidae and Bovidae) in order to have a better picture of which herbivores lived in Central Italy from the Pliocene to the Holocene (Fig. 7A): while brachydonts are in small percentage and almost always present, mesodonts are characterized by a good percentage of species that, only in the late Aurelian, tends to decrease. Hypsodonts show a more articulated trend: they first form a block and then

show a minimum at the end of each Mammal Age. A remarkable increase of the hypsodonts, in respect to the mesodonts, characterizes the middle and late Villafranchian and the Aurelian.

The same trend, can be seen in the previous diagram, but more detailed, and it is obtained considering each Faunal Unit (Fig. 7B): the remarkable prevalence of the hypsodonts in respect to the mesodonts in the Middle and Late Pleistocene is highlighted.

The simple hypsodonts/mesodonts-ratio is pointed out in Figure 8, wherein, above the value 1, the temporal intervals characterized by the prevalence of hypsodonts are reported. This could indicate that the long temporal intervals in which the hypsodonts clearly prevail (e.g., the Montopoli and Pirro F.U.'s, the Aurelian M.A.) correspond to the prevalence of the open lands.

CONCLUSIONS

Some conclusive considerations from the quantitative analysis of the macromammal taxa found in Central Italy can be pointed out.

The number of macromammal species present in Central Italy from the early Villafranchian to the

late Aurelian is fairly close to the trend defined for all of the Peninsula's deposits and it seems to lean towards a moderate increase (Fig. 2); the lowest values of the number of recorded taxa, therefore, the lower values of biodiversity, coincide, as was logically expected, with the passage of one Mammal Age to another. The rise of the same biodiversity in the entire temporal arc considered, but much more emphasized from the Galerian to the late Aurelian, can depend on different factors, one of which could be connected to structural factors: the progressive geological and physiographic development of the Peninsula provided to diversify the ecological niches and/or microclimates. In fact, during the Pliocene and earliest Pleistocene (early and middle Villafranchian biochrons), it is possible to observe an environmental uniformity which will successively tend to decrease in the last one million year. This change enabling the diffusion and the adaptation of a greater number of species.

On the contrary, the paleobotanical data provide clear evidence of a progressive decrease in number of arboreal species from the Middle Pliocene to the end of the Early Pleistocene; therefore, the biodiversity of the arboreal plants seems to initially follow a trend that is opposed to the preceding that was recorded for the mammals. This can be explained by the fact that most of these arboreal species represented evergreen forms connected to groups of "subtropical", humid forests, documented for the last time in the Gelasian in Central Italy, in association with mammals from the Montopoli Faunal Unit. In Calabria, even with an impoverished flora, the "subtropical", humid forest, instead, continues until the beginning of the Early Pleistocene (Olivola and Tasso Faunal Units).

The palaeobotanical documentation of the progressive increase of open areas, which until the end of the Piacenzian had to be nearly all absent or limited to the fluvial areas, is particularly important. From the beginning of the Piacenzian-Gelasian transition (apart from an evident dropping of the annual mean temperature with the presence of conifer in the planes) a first sign of the vegetation opening up is recorded (Bertini 2006), which is found in the macromammal renewals of Toscana (Montopoli and Tasso-Olivola Faunal Units). From this point

on the climatic oscillations caused rapid variations in the vegetation cover and a progressive disappearance of the floral elements that ill-suited for unstable conditions. Nevertheless, the pollen data indicate that the steppic phases, which are longer lasting and frequent in Southern Italy, developed only during some extreme glacial peaks (Russo Ermolli *et al.* 1995; Russo Ermolli 2000; Pontini & Bertini 2000; Capraro *et al.* 2005).

The environmental differences in the Middle and Late Pleistocene between the Tyrrhenian and Adriatic area cannot be clearly defined; first because the Adriatic data, as noted above, is very sporadic; and second (independent of the poor Adriatic data), because the large part of the mammal taxa in Central Italy seem, nevertheless, to prefer the wider and diversified territories of the Tyrrhenian slopes. In cases where the Adriatic data is more complete, it is possible, however, to observe a trend that is fairly close to that of the Tyrrhenian; thus, one can conclude that the different climates of the two areas did not influence the trend of the taxa numbers or the abundance of populations.

In addition, a great number of herbivorous macromammals came from Asia, and it would perhaps be logical to expect a larger number of first occurrences (FO) of taxa in the Adriatic corridor; however, the analytical data confirm that the number of first occurrences in the Tyrrhenian side is greater. To justify this trend it can be hypothesized that in interglacial moments, the Tosco-Emilian Apennines had allowed the taxa coming from the northeast to enter and spread out into the more diversified Tyrrhenian side, whereas during the glacial periods the narrow Ligurian corridor, which functioned as a point of passage for some of the Italian species, needs to be revalued.

The migrations and the relative survival of the taxa on the Italian peninsula happened in a unique way: the species that entered late and with some difficulty through mountain passes during the climatic renewals tend to remain in Italy for a longer time and survive in the territory that became a refuge zone of continental Europe, and in several instances, even a sort of "trap". These particular conditions permit the Italian mammal fauna to at times develop morphotypes with a certain degree

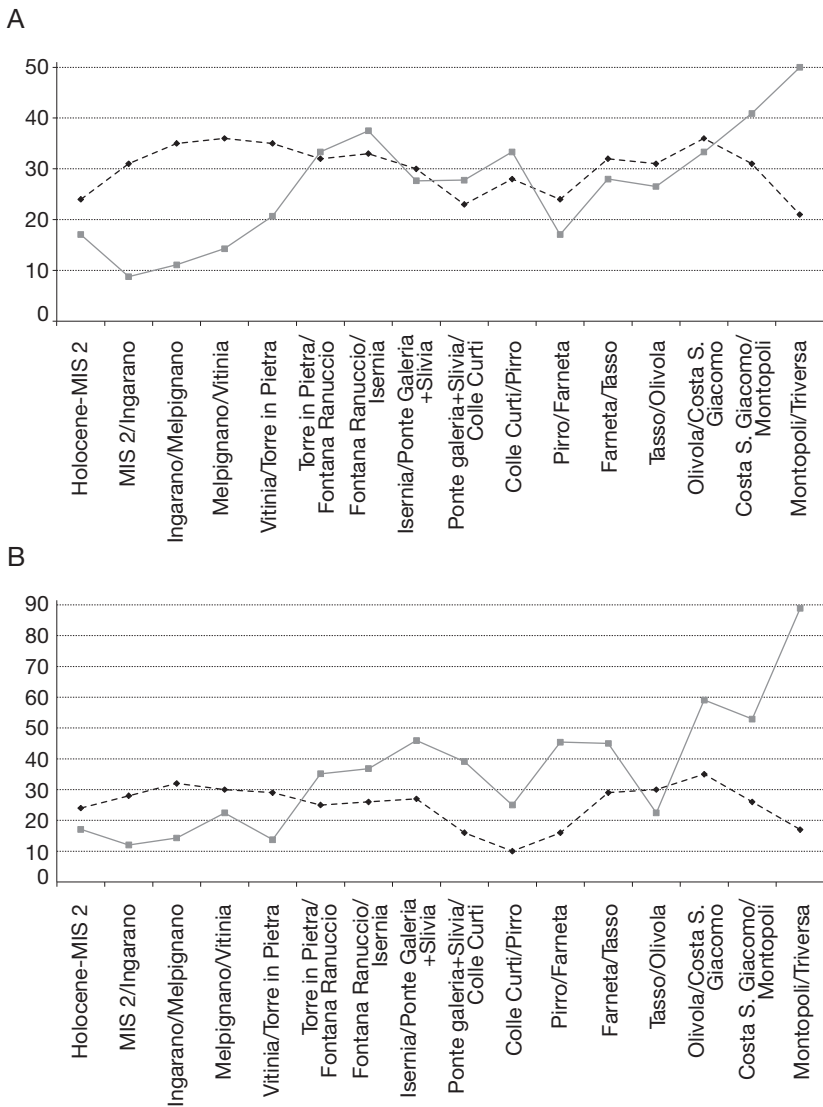


Fig. 9. — **A**, comparison between the quantity of taxa (continuous line) and the turnover indices (dashed line) for the temporal intervals comprised in the Faunal Units for Italy; **B**, comparison between the quantity of taxa (continuous line) and the turnover indices (dashed line) for the temporal intervals comprised in the Faunal Units for Central Italy. In abscissa the values of number of taxa and turnover index. Abbreviation: **MIS 2**, Marine Isotope Stage 2.

of endemism, which in some cases favors the appearance of particular taxa (*Elephas antiquus italicus* Osborn, 1931, *Cervus elaphus rianensis* Leonardi & Petronio, 1974, *C. e. aretinus* Azzaroli, 1947, etc.). Due to the mild climate of the central part of the peninsula, the taxa were almost exclusively typical

forms of Cervidae, like those of the *Axis* genus (with the species *A. lyra*, *A. nestii* and *A. eurygonos*) and the *Dama* genus that already established itself on the Peninsula in the Isernia Faunal Unit and that only in the Hoxinian late-interglacial does it reach Great Britain (Sutcliffe 1964), leaving sporadic

traces of its existence throughout the European continent.

The biodiversity, which shows an increasing trend from the Galerian to the late Aurelian, has a sharp drop in the last 30 000 years, probably due to the human activities that impacted the environment, together with the strong climatic cooling of the last pleniglacial and the subsequent abrupt warming.

The relative rise of the quantity of carnivorous mammals has already been pointed out (Fig. 3); here it can be added that the majority of carnivorous in the last 500 000 years included predators that are of medium and small dimensions: considering even in this case that much data is missing for the oldest findings, it can be hypothesized that the higher diversity of the ecological niches has favored the small carnivores, thanks also to a high number of small-sized prey.

The analyses of the values of the first and last occurrences, together with the faunal renewals in the intervals between the several Faunal Units and the Mammal Ages (Fig. 6), allows a comparison to be done in respect to the turnover line and the quantity of recorded mammal taxa (Fig. 9A). The relative turnover lines (continuous line) in all of the peninsula and the abundance of taxa line in the same temporal interval (dashed line) relate in some way: even in Figure 9B, which summarizes the relative data of the taxa and of the turnover in Central Italy, it is possible to observe the same trend: maximum values of the abundance of taxa correspond to the minimum values of the turnover, even if in an approximate way; this can signify, therefore, that in moments of rich biodiversity there is a low faunal renewal and vice versa.

The relative abundance of brachydonts, mesodonts and hypsodonts is related to a progressive reduction of the wooded areas. From the Pliocene to the Holocene the wooded areas started to thin out into clearings and prairies; this phenomenon is more evident in the last one million year (Fig. 7).

To explain how the abundance of mammals, indicative of open lands, can compare with the prevalence of humid forests in the paleobotanical record, it is necessary to hypothesize that the population of grazing mammals (which increased in numbers during the steppic phases) could have

wielded – during the more humid, climatic phases – an impact on the vegetation, impeding the growth of arboreal plants on fairly widespread areas and favoring the growth of herbaceous plants.

The great faunal renewals, which correspond, as stated before, to the passage between the Villafranchian, the Galerian and the Aurelian do not seem to have been caused only by strong climatic turnovers; nevertheless, these changes, together with strong floral changes, could have had a significant role in the distribution and then in the diffusion of the many ecological niches. An interesting issue that asks for further in-depth examination is represented by the turnover lines that seem to coincide (Figs 1; 9) with the principal moments of paleomagnetic inversion of the Pliocene-Pleistocene (the passage Gauss-Matuyama, the subchrons Olduvai and Jaramillo).

At the moment it can possibly be asserted that the principal changes of biodiversity during the Pliocene and Pleistocene were caused by all of these factors; to these, for the last part of the Pleistocene, the influence of human activities, by *Homo neanderthalensis* (King, 1864) first and then by *Homo sapiens* Linnaeus, 1758 later, could have directly or indirectly had an influence on the ecosystems.

Acknowledgements

This work has been supported by MIUR PRIN 2006 grants (resp. C. Petronio).

REFERENCES

- ACANFORA M. O. 1962. — Gli scavi di Valle Ottara presso Cittaducale. *Bollettino Paleontologia Italiana* 71/72: 101-154.
- ALHAIQUE F. 1996. — Sfruttamento dei piccoli mammiferi e dei carnivori nel Paleolitico superiore di Grotta Polesini, in Peretto C. & Milliken S. (eds), *L'adattamento umano all'ambiente, passato e presente. Atti XI congresso degli Antropologi Italiani*. Abaco, Forlì: 209, 210.
- ALHAIQUE F., BIONDI S., CASSOLI P. F., RECCHI A. & TAGLIACCOZZO A. 1988. — Modifications in the exploitation of animal resources between the Middle Palaeolithic and the Aurignacian at Grotta del Fossellone (Monte Circeo, Italy). *Atti UISPP XIII* 6 (1): 571-576.

- ALHAIQUE F., BIETTI A., CAPASSO BARBATO L., GRIMALDI S., KOTSAKIS T., KUHN S., LEMORINI C., MANZI G., RECCHI A., SCHWARCHZ H. P. & STINER M. 1998. — Settlement patterns and subsistence strategies in the la mousterian site of Grotta Breuil (Mt. Circeo, Italy). *Atti UISPP XIII* 6 (1): 221-228.
- ARZARELLO M., BELARDINELLI L., MINELLI A., PAVIA M., RUFO E., SALA B., THUN HOHENSTEIN U. & PERETTO C. 2004. — Il sito paleolitico medio di Grotta Reali (Rocchetta del Volturno, Molise, Italia). *Rivista Scienze Preistoriche* 54: 249-269.
- ARZARELLO M., MARCOLINI F., PAVIA G., PAVIA M., PETRONIO C., PETRUCCI M., ROOK L. & SARDELLA R. 2007. — Evidence of earliest human occurrence in Europe: the site of Pirro Nord (Southern Italy). *Naturwissenschaften* 94 (2): 107-112.
- AZZAROLI A. 1977. — The Villafranchian stage in Italy and the Plio-Pleistocene boundary. *Giornale di Geologia* 41: 61-79.
- BENVENUTI M., BERTINI A., CONTI C. & DOMINICI S. 2007. — Integrated analyses of litho- and biofacies in a Pliocene cyclothem, alluvial to shallow marine succession (Tuscany, Italy). *Geobios* 40: 143-158.
- BERTINI A. 2000. — Pollen record from Colle Curti and Cesi: Early and Middle Pleistocene mammal sites in the Umbro-Marchean Apennine Mountains (central Italy). *Journal Quaternary Sciences* 15 (8): 825-840.
- BERTINI A. 2006. — The Northern Apennines palynological record as a contribute for the reconstruction of the Messinian palaeoenvironments. *Sedimentary Geology* 188/189: 235-258.
- BIANUCCI G. P. 1980. — Ricerche speleologiche alla Buca dei Ladri (Asciano-Pisa). *Atti Società Toscana di Scienze Naturali Memorie S.A* 87: 261-274.
- BIETTI A. 1984. — Primi risultati dello scavo nel giacimento epigravettiano finale di Riparo Salvini (Terracina, Latina). *Atti IIPP XXIV*: 195-205.
- BILLIA M. E. & PETRONIO C. 2009. — Selected records of *Stephanorhinus kirchbergensis* (Jäger, 1839) (Mammalia, Rhinocerotidae) in Italy. *Bollettino della Società Paleontologica Italiana* 48 (1): 21-32.
- BOLOGNA P., DI STEFANO G., MANZI G., PETRONIO C., SARDELLA R. & SQUAZZINI E. 1994. — Late Pleistocene mammals from a the Melpignano (LE) "Ventarole": preliminary analysis and correlations. *Bollettino della Società Paleontologica Italiana* 33 (2): 263-274.
- BOSCATO P. 1996. — Vado all'Arancio (Massa Marittima, GR). Studio delle faune. *Rassegna di Archeologia* 13: 159-176.
- BOSCATO P., CATTANI L., CUDA M. T. & MARTINI F. 2001. — Il Musteriano della grotta di S.Francesco a Belverde di Cetona. *Rivista Scienze Preistoriche* 51: 3-48.
- BULGARELLI G. M. & TAGLIACCOZZO A. 1984. — Il paleolitico superiore di Ponte Sfondato (Montopoli Sabina). *Atti IIPP XXIV*: 175-181.
- CALOI L. & PALOMBO M. R. 1987. — I grandi mammiferi del Pleistocene superiore di Grotta Barbara (Monte Circeo, Lazio meridionale). *Bollettino Servizio Geologico d'Italia* 106: 3-58.
- CALOI L., PALOMBO M. R. & PETRONIO C. 1979. — Cenni preliminari sulla fauna di Cava Redicicoli (Roma). *Bollettino Servizio Geologico d'Italia* 100: 189-198.
- CALOI L., PALOMBO M. R. & PETRONIO C. 1980. — La fauna quaternaria di Sedia del Diavolo (Roma). *Quaternaria* 22: 177-209.
- CALOI L., COCCOLINI G. B. L., MUSSI M., PALOMBO M. R., VITAGLIANO S. & ZAMPETTI D. 1989. — Le Moustérien du Latium (Italie centrale): archéologie milieu naturel, chronologie. *L'Anthropologie* 93 (1): 73-98.
- CAPASSO BARBATO L., CUGGANI M. C. & PETRONIO C. 1982. — I macromammiferi del Pleistocene superiore della grotta di Monte Cucco (Sigillo, Perugia). *Bollettino Servizio Geologico d'Italia* 103: 105-132.
- CAPASSO BARBATO L., DI STEFANO G., PETRONIO C. & SARDELLA R. 1998. — Pleistocene mammal faunas from Ponte Molle (Rome). *Quaternary International* 47/48: 73-75.
- CAPASSO BARBATO L., MINIERI M. R. & SCARANO M. 1991. — Paleogeografia dei mammiferi "freddi" del Pleistocene medio-superiore e superiore italiano. *Atti Accademia Peloritana dei Pericolanti* 67 supplemento 1: 231-259.
- CAPRARO L., ASIOLI A., BERTOLDI R., CHANNELL J. E. T., MASSARI F. & RIO D. 2005. — Climatic patterns revealed by pollen and oxygen isotope records across the Matuyama-Brunhes boundary in the central Mediterranean (southern Italy). *Geological Society Special Publications* 247: 159-182.
- CASSOLI P. F. 1976. — Upper Palaeolithic fauna at Palidoro (Rome): 1955 excavations. *Quaternaria* 19: 187-196.
- CASTELLETTI L., MASPERO A. & TOZZI C. 1994. — Il popolamento della Valle del Serchio (Toscana settentrionale) durante il Tardiglaciale würmiano e l'Olocene antico, in Biagi P. & Nandris J. (eds), *Highland zone exploitation in southern Europe. Monografie di Natura Bresciana* 20: 189-204.
- CAVALLO P. & MARTINETTO E. 2001. — Flore carpologiche del Pliocene di Castelletto Cervo (Biella). *Bollettino del Museo Regionale di Scienze Naturali di Torino* 18 (2): 277-343.
- CAZZELLA A. & MOSCOLONI M. 1984. — Tracce di insediamento del Paleolitico superiore a Tor Vergata (Roma). *Atti IIPP XXIV*: 165-173.
- CERILLI E. & BROCATO G. 1998. — The Upper Palaeolithic deposit of Valle Arcione (Castel d'Asso, Viterbo, Italy). *Atti UISPP XIII* 2: 681-685.
- CILLI C., MALERBA G. & TOZZI C. 1998. — Analyse archéozoologique et modifications de surface des restes fauniques de deux sites du Paléolithique supérieur de

- Toscane (Italie). *Atti UISPP XIII* 2: 675-679.
- COLTORTI M., FERAUD G., MARZOLI A., PERETTO C., TON-THAT T., VOINCHET P., BAHAIN J.-J., MINELLI A. & THUN HOHENSTEIN U. 2005. — New $^{40}\text{Ar}/^{39}\text{Ar}$, stratigraphic and palaeoclimatic data on the Isernia La Pineta Lower Palaeolithic site, Molise, Italy. *Quaternary International* 131: 11-22.
- CREMONESI G. 1968. — Contributo alla conoscenza della preistoria del Fucino: la Grotta di Ortucchio e la Grotta La Punta. *Rivista Scienze Preistoriche* 23: 145-204.
- DEL CAMPANA D. 1954. — Carnivori quaternari della Tecchia e della Caverna di Equi nelle Alpi Apuane (Mustelidi, Canidi, Felidi). *Palaeontographia italica* 44 (2): 1-42.
- DI CANZIO E. & PETRONIO C. 2001. — Osservazioni sulla fauna a vertebrati pleistocenici della Grotta Cola (Abruzzo, Aquila). *Bollettino della Società Paleontologica Italiana* 40 (1): 105-114.
- DI CANZIO E., BEDETTI C., PETRONIO C. & SARDELLA R. 2003. — Middle Pleistocene vertebrate fauna from Cretone (Sabina, Latium). *Bollettino della Società Paleontologica Italiana* 42: 129-132.
- DI STEFANO G. & PETRONIO C. 2000. — Systematics and evolution of the Eurasian Plio-Pleistocene tribe Cervini (Artiodactyla, Mammalia). *Geologica Romana* 36: 311-334.
- FABIANI R. 1922. — La fauna mammalogica della "Buca del Tasso". *Archivio per l'Antropologia e l'Etnologia* 52: 10-20.
- FAVRE E., FRANÇOIS L., FLUTEAU F., CHEDDADI R., THEVENOD L. & SUC J.-P. 2007. — Messinian vegetation maps of the Mediterranean region using models and interpolated pollen data. *Geobios* 40 (3): 433-443.
- FOLLIERI M., MAGRI D. & SADORI L. 1988. — 250 000-year pollen record from Valle di Castiglione (Roma). *Pollen et Spores* 30 (3, 4): 329-356.
- GIROTTI O., CAPASSO BARBATO L., ESU D., GLIOZZI E., KOTSAKIS A., MARTINETTO E., PETRONIO C., SARDELLA R. & SQUAZZINI E. 2003. — The section of Torre Picchio (Terni, Umbria, Central Italy): A Villafranchian site rich in Mammals, Molluscs, Ostracods and Plants. *Rivista Italiana di Paleontologia e Stratigrafia* 109 (1): 77-98.
- GIUSTIZIA F. 1979. — Il deposito musteriano nel Riparo I Grottini presso Balascio (L'Aquila). Nota preliminare. *Atti Società Toscana di Scienze Naturali Memorie S.A* 86: 189-201.
- GLIOZZI E., ABBAZZI L., ARGENTI P., AZZAROLI A., CALOI L., CAPASSO BARBATO L., DI STEFANO G., ESU D., FICcarelli G., GIROTTI O., KOTSAKIS T., MASINI F., MAZZA P., MEZZABOTTA C., PALOMBO M. R., PETRONIO C., ROOK L., SALA B., SARDELLA R., ZANALDA E. & TORRE D. 1997. — Biochronology of selected Mammals, Molluscs and Ostracods from the Middle Pliocene to the Late Pleistocene in Italy. The state of the art. *Rivista Italiana di Paleontologia e Stratigrafia* 103: 369-388.
- GRAZIOSI P. 1928. — La Grotta di Talamone. *Archivio per l'Antropologia e l'Etnologia* 58: 122-152.
- GRAZIOSI P. 1944. — La Grotta all'Onda secondo gli scavi dell'Istituto Italiano di Paleontologia Umana (1931). *Archivio per l'Antropologia e l'Etnologia* 64: 73-120.
- GRIFONI R. & RADMILLI A. M. 1964. — La Grotta Maritza e il Fucino prima dell'età romana. *Rivista Scienze Preistoriche* 19: 53-127.
- GUÉRIN C., FAURE M., ARGANT A., ARGANT J., CREGUT-BONNOURE E., DEBARD E., DELSON E., EISENMANN V., HUGUENY M., LIMONDIN-LOZOUET N., MARTIN-SUAREZ E., MEIN P., MOURER-CHAUVIRÉ C., PARENTI F., PASTRE J.-F., SEN S. & VALLI A. M. F. 2004. — Le gisement pliocène supérieur de Saint-Vallier (Drôme, France): synthèse biostratigraphique et paléoécologique, in Faure M. & Guérin C. (eds), Le gisement pliocène final de Siant-Vallier (Drôme, France). *Geobios* 37 (mémoire spécial 26): 349-360.
- GUERRESCHI A., SILVESTRINI M., PERESANI M., ESU D., GALLINI V., MAGNATTI M. & MURATORI S. 2005. — I depositi epigravettiani del sito 1 di Cava Romita: cronologia, faune, industria litica. *Atti IIPP XXXVIII*: 117-130.
- KOTSAKIS T., ABBAZZI L., ANGELONE C., ARGENTI P., BARISONE G., FANFANI F., MARCOLINI F. & MASINI F. 2003. — Plio-Pleistocene biogeography of Italian mainland micromammals, in Reumer J. W. F. & Wessels W. (eds), Distribution and migration of Tertiary mammals in Eurasia. A volume in honour of Hans de Bruijn. *Deinsea* 10: 313-342.
- KOTSAKIS T., PETRONIO C., ANGELONE C., BELLUCCI L., MARCOLINI F., SALARI L. & SARDELLA R. 2008. — Changes in the Late Villafranchian Mammal assemblages (from Farneta to Pirro FU, Early Pleistocene) of Italy. Abstract 33rd *International Geological Congress*, Oslo 6-14 august 2008.
- LEROY S. A. G. 2007. — Progress in palynology of the Gelasian-Calabrian Stages in Europe: ten messages. *Revue de Micropaléontologie* 50: 293-308.
- LINDSAY E. H., OPDYKE N. D. & JOHNSON N. M. 1980. — Pliocene dispersal of the horse *Equus* and late Cenozoic mammal dispersal events. *Nature* 287: 135-138.
- LONA F. & BERTOLDI R. 1973. — La storia del Plio-Pleistocene italiano in alcune sequenze vegetazionali lacustri e marine. *Atti dell'Accademia Nazionale dei Lincei Memorie serie 8*, 11 (1): 1-47.
- MAI D. H. 1994. — Fossile Koniferenreste in der meridionalen Zone Europas. *Feddes Repertorium*, 105 (3, 4): 207-227.
- MAI D. H. 1995. — *Tertiäre Vegetationsgeschichte Europas*. Gustav Fischer, Jena, 691 p.
- MARTINETTO E. 1996. — Pliocene vegetation at the western margin of the Po Basin. *Allionia* 34: 349-355.

- MARTINETTO E. 1999. — Chronological framing of Pliocene to Early Pleistocene plant macrofossil assemblages from northern Italy. *Acta Palaeobotanica Suppl.* 2: 503-511.
- MARTINETTO E. 2001. — Studies on some exotic elements of the Pliocene floras of Italy. *Palaeontographica, Abt. B*, 259: 149-166.
- MARTINETTO E. & MAI D. H. 1996. — Macrofossili vegetali, in Carraro F. (ed.), Revisione del Villafranchiano nell'area-tipo di Villafranca d'Asti. *Il Quaternario* 9 (1): 73-79.
- MARTINETTO E., SCARDIA G. & VARRONE D. 2007. — Magnetobiostratigraphy of the Stura di Lanzo Fossil Forest succession (Piedmont, Italy). *Rivista Italiana di Paleontologia e Stratigrafia* 113 (1): 109-125.
- MAZZA P. A., BERTINI A. & MAGI M. 2004. — The late Pliocene site of Poggio Rosso (central Italy): taphonomy and paleoenvironment. *Palaios* 19 (3): 227-248.
- MAZZINI I., PACCARA P., PETRONIO C. & SARDELLA R. 2000. — Geological Evolution and Biochronological Evidence of the Monte Riccio Section. *Rivista Italiana di Paleontologia e Stratigrafia* 106 (2): 247-256.
- MERRIL R. T., MCELHINNY M. W. & MCFADDEN P. L. 1996. — *The Magnetic Field of the Earth: Paleomagnetism, the Core and the Deep Mantle*. San Diego Academic Press, San Diego, 541 p.
- MONEGATTI P., CANALI G., BERTOLDI R. & ALBIANELLI A. 2002. — The classical Late Piacenzian Monte Falcone-Rio Crevaiese section (Northern Italy): palynological evidence and biomagnetostratigraphic constraints for climatic cyclicity and local mollusc extinctions. *Geobios* (mémoire spécial 24): 219-227.
- NAPOLEONE G., AZZAROLI A. & MAZZINI M. 2003. — Magnetostratigraphic significance of the end-pliocene age of the new found locality of Poggio Rosso in the Upper Valdarno, for dating its late Villafranchian faunas. *Rivista Italiana di Paleontologia e Stratigrafia* 107 (2): 287-296.
- PALMARELLI A. & PALOMBO M. R. 1981. — Un cranio di *Coelodonta antiquitatis* (Blumenbach) (Rhinocerotidae) del Pleistocene superiore del Monte Circeo (Lazio meridionale). *Bollettino Servizio Geologico d'Italia* 102: 281-312.
- PALOMBO M. R. & FERRETTI M. P. 2005. — Elephant fossil record from Italy: knowledge, problems, and perspectives. *Quaternary International* 126-128: 107-136.
- PALOMBO M. R., AZANZA B. & ALBERDI M. T. 2002. — Italian mammal biochronology from the Latest Miocene to the Middle Pleistocene: a multivariate approach. *Geologica Romana* 36: 335-368.
- PETRONIO C. 1995. — Note on the taxonomy of Pleistocene Hippopotamuses. *IBEX Journal of Mountain Ecology* 3: 53-55.
- PETRONIO C. & SARDELLA R. 1999. — Biochronology of the Pleistocene mammal fauna from Ponte Galeria (Rome) and remarks on the Middle Galerian faunas. *Rivista Italiana di Paleontologia e Stratigrafia* 105: 155-164.
- PETRONIO C., ARGENTI P., CALOI L., ESU D., GIROTTI O. & SARDELLA R. 2002. — Updating Villafranchian mollusc and mammal faunas of Umbria and Latium (Central Italy). *Geologica Romana* 36: 369-387.
- PETRONIO C., ANZIDEI A. P., BEDETTI C., BONA F., DI CANZIO E., GENTILI S., MAZZA P., PALOMBO M. R., PAVIA M., SALARI L., SARDELLA R. & TINTORI A. 2005. — Le faune a mammiferi del Plio-Pleistocene, in Bonfiglio L. (ed.), Paleontologia dei Vertebrati in Italia. *Memorie Museo Civico Storia Naturale di Verona, II S., Scienze della Terra* 6: 183-218.
- PETRONIO C., DI CANZIO E. & SALARI L. 2007. — The Late Pleistocene and Holocene Mammals in Italy: new biochronological and paleoenvironmental data. *Palaeontographica, Abt. A*, 279: 147-157.
- PITTI C., SORRENTINO C. & TOZZI C. 1976. — L'industria di tipo paleolitico superiore arcaico della Grotta La Fabbrica (Grosseto). Nota preliminare. *Atti Società Toscana di Scienze Naturali Memorie S.A.* 83: 174-201.
- PITTI C. & TOZZI C. 1971. — La Grotta del Capriolo e la Buca della Iena presso Mommio (Camaioere, Lucca). *Rivista Scienze Preistoriche* 26: 213-258.
- PONTINI M. R. & BERTINI A. 2000. — Late Pliocene vegetation and climate in central Italy: high-resolution pollen analysis from the Fosso Bianco succession (Tiberino Basin). *Geobios* 33: 519-526.
- RADI G. 1982. — L'industria Bertoniana del riparo di Venere (L'Aquila). *Atti Società Toscana di Scienze Naturali* 89: 189-207.
- RADMILLI A. M. 1977. — *Storia dell'Abruzzo dalle origini all'età del bronzo*. Collana Studi Paleontologici, Giardini, Pisa, 464 p.
- RADMILLI A. M., ROMAGNOLI L. & TONGIORGI E. 1955. — Il deposito eolico sul versante occidentale del promontorio di Ansedonia e la fauna fossile della grotta Rose Mary. *Atti Società Toscana di Scienze Naturali* 62: 73-87.
- RAVAZZI C. 2002. — Late Quaternary history of spruce in Southern Europe. *Review of Palaeobotany and Palynology* 120 (1, 2): 131-177.
- RAVAZZI C., PINI R., BREDA M., MARTINETTO E., MUTTONI G., CHIESA S., CONFORTINI F. & EGLI R. 2005. — The lacustrine deposits of Fornaci di Ranica (late Early Pleistocene, Italian Pre-Alps): stratigraphy, palaeoenvironment and geological evolution. *Quaternary International* 131: 35-58.
- ROOK L. & SARDELLA R. 2005. — *Hystrix refossa* Gervais, 1852 from Pirro Nord (Early Pleistocene, Southern Italy). *Rivista Italiana Paleontologia e Stratigrafia* 111: 489-496.
- ROOK L., MARTÍNEZ-NAVARRO B. & HOWELL F. C. 2004. — Occurrence of *Theropithecus* sp. in the Late

- Villafranchian of Southern Italy and implication for Early Pleistocene "out of Africa" dispersals. *Journal of Human Evolution* 47: 267-277.
- RUFFO M. 1995. — Origine degli insiemi faunistici nei vari livelli deposizionali della Grotta delle Capre – S. Felice Circeo (LT) – 1993. *Atti 1° Conv. Naz. Archeozoologia, Padusa Quaderni* 1: 109-123.
- RUSSO ERMOLLI E. 2000. — Pollen analysis of the Acereno palaeo-lacustrine succession (middle Pleistocene, southern Italy). *Geological Society Special Publications* 181: 151-159.
- RUSSO ERMOLLI E., JUVIGNÉ É., BERNASCONI S., BRANCACCIO L., CINQUE A., LIRER L., OZER A. & SANTANGELO N. 1995. — Le premier stratotype continental de quatre stades isotopiques successifs du Pléistocène moyen pour le bassin méditerranéen septentrional: le Vallo di Diano (Campanie, Italie). *Comptes Rendus de l'Académie des Sciences de Paris* 321 (2a): 877-884.
- RUSTIONI M., MAZZA P. & BALESTRI M. 1999. — The Middle-Late Pleistocene mammal fauna from Montignoso (Leghorn, Central Italy). *Il Quaternario* 12 (1): 105-111.
- SARDELLA R., ABBAZZI L., ARGENTI P., AZZAROLI A., CALOI L., CAPASSO BARBATO L., DI STEFANO G., FICCARELLI G., GLIOZZI E., KOTSAKIS T., MASINI F., MAZZA P., MEZZABOTTA C., PALOMBO M. R., PETRONIO C., ROOK L., SALA B. & TORRE D. 1998. — Mammal Faunal Turnover in Italy from the Middle Pliocene to the Holocene. *Mededelingen Nederlands Instituut voor Toegepaste Geowetenschappen TNO* 60: 499-512.
- SEGRE A. G. & ASCENZI A. 1956. — Giacimenti del paleolitico superiore e del bronzo nei travertini di Cisterna (Latina). *Rivista di Antropologia* 43: 367-411.
- SEGRE A. G., BIDDITTU I. & CASSOLI P. F. 1984. — Il bacino paleolacustre di Sora (Frosinone) e i suoi giacimenti musteriani. *Atti IIPP XXIV*: 149-154.
- SEGRE NALDINI E. 1984. — Il Musteriano di Grotta della Cava, Sezze Romano (Latina). *Atti IIPP XXIV*: 141-147.
- SHAKRYL A. K. 1990. — Development of Lauraceae in the Colchidian refuges, in Knobloch E. & Kvaček Z. (eds), *Proceedings of the Symposium Palaeofloristic and Palaeoclimatologic Changes in the Cretaceous and Tertiary*. Geological Survey Publisher, Prague: 311-313.
- SOMMER R. & BENECKE N. 2004. — Late- and post-glacial history of the Mustelidae in Europe. *Mammal Review* 34 (4): 249-284.
- SUC J.-P. & BESSAIS E. 1990. — Pérennité d'un climat thermoxérique en Sicile, avant, pendant et après la crise de salinité messinienne. *Comptes Rendus de l'Académie des Sciences de Paris* 310 (II): 1701-1707.
- SUC J.-P. & POPESCU S.-M. 2005. — Pollen records and climatic cycles in the north Mediterranean region since 2.7 Ma. *Geological Society Special Publications* 247: 147-158.
- SUC J.-P., BERTINI A., COMBOURIEU-NEBOUT N., DINIZ F., LEROY S., RUSSO-ERMOLLI E., ZHENG Z., BESSAIS E. & FERRIER J. 1995a. — Structure of West Mediterranean and climate since 5.3 Ma. *Acta Zoologica Cracoviensia* 38 (1): 3-16.
- SUC J.-P., DINIZ F., LEROY S., POUMOT C., BERTINI A., DUPONT L., CLET M., BESSAIS E., ZHENG Z., FAUQUETTE S. & FERRIER J. 1995b. — Zanclean (\approx Brunsumian) to early Piacenzian (\approx early-middle Reuverian) climate from 4° to 54° north latitude (West Africa, West Europe and West Mediterranean areas). *Mededelingen Rijks Geologische Dienst* 52: 43-56.
- SUTCLIFFE A. 1964. — The mammalian fauna, in Ovey C. D. (ed.), *The Swanscombe skull. Royal Anthropological Institute Occasional Papers* 20: 85-111.
- TOZZI C. 1970. — La Grotta di S. Agostino (Gaeta). *Rivista Scienze Preistoriche* 25: 3-87.
- TOZZI C. 1974. — L'industria musteriana della Grotta di Gosto sulla Montagna di Cetona. *Rivista Scienze Preistoriche* 29: 271-304.
- VITAGLIANO S. 1984. — Nota sul Pontiniano della Grotta dei Moscerini, Gaeta (Latina). *Atti IIPP XXIV*: 155-164.
- WILKENS B. 1991. — *Resti faunistici ed economia preistorica nel bacino del Fucino. Atti del convegno di archeologia "Il Fucino e le aree limitrofe nell'antichità"*. Archeoclub d'Italia, Marsica: 147-153.

Submitted on 22 May 2009;
accepted on 19 November 2010.

APPENDICES

TABLE 1. — Early and Middle Villafranchian mammal faunas from selected localities in Central Italy. x, local record of each taxon; *, total of local records for each taxon. Abbreviations: **EV**, early Villafranchian; **MV**, middle Villafranchian; **CSG**, Coste San Giacomo; **Mon**, Montopoli; **Tri**, Triversa.

Localities	Braga	Spoletto	S. Croce	Montopoli	Colleparado	Valle Catenaccio	Coste S. Giacomo	Cava Toppetti	Castel S. Pietro	Total*
Mammal Ages	EV			MV						
Faunal Units	Tri		Mon	CSG						
<i>Anancus arvernensis</i>		x	x	x			x		x	5
<i>Mammuth borsoni</i>			x							1
<i>Tapirus arvernensis</i>	x	x	x							3
<i>Homotherium latidens</i>	x									1
<i>Mammuthus gromovi</i>				x						1
<i>Stephanorhinus janvireti</i>				x	x					2
<i>Lynx issiodorensis</i>				x						1
<i>Stephanorhinus etruscus</i>				x			x		x	4
<i>Equus livenzovensis</i>				x				x		2
<i>Axis lyra</i>				x	x	x	x	x		5
<i>Croizetoceros ramosus</i>				x						1
<i>Eucladoceros falconeri</i>				x						1
<i>Gazella borbonica</i>				x		x	x			3
<i>Leptobos stenometopon</i>				x						1
<i>Acinonyx pardinensis</i>				x						1
<i>Nyctereutes megamastoides</i>				x	x					2
<i>Pliocrocuta perrieri</i>				x		x				2
<i>Sus minor</i>					x					1
<i>Hemitragus sp.</i>					x					1
<i>Megantereon cultridens</i>					x					1
<i>Mammuthus meridionalis meridionalis</i>						x	x			2
<i>Eucladoceros teguliensis</i>						x	x			2
<i>Equus stenonis</i>							x			1
<i>Gazellospira torticornis</i>							x			1
<i>Leptobos merlai furtivus</i>							x	x	x	3
<i>Galogoral meneghini</i>							x			1
<i>Canis etruscus</i>							x			1
<i>Vulpes alopecoides</i>							x			1
<i>Procapreolus sp.</i>								x		1
Total	2	2	3	13	6	5	12	5	3	

TABLE 2. — Late Villafranchian mammal faunas from selected localities in Central Italy. x, local record of each taxon; *, total of local records for each taxon. Abbreviations: LV, late Villafranchian; Far, Farneta; Oli, Olivola; Pir, Pirro; Tas, Tasso.

Localities	Valdamo superiore 1	Olivola	Bandita di Giove	Capitone	Rome-Monte Mario	Villa S.Faustino	Torre Picchio	Valdamo superiore 2	Colle Valenza	Rieti-dintorni	Matassino	Bocchignano	Pantalla	Fontana acetosa-Anagni	Monte Riccio	Ellera Corciano	Fighille	Mugello	Val di Chiana	Pietrafitta	Montecastrilli	Capena	Roma-Redicicoli 1	Total*	
	LV																								
Mammal Age	LV																								
Faunal Units	Oli					Tas							Far			Pir									
<i>Mammuthus meridionalis meridionalis</i>	x	x	x		x	x	x	x	x	x				x	x									11	
<i>Stephanorhinus etruscus</i>	x	x	x	x		x	x	x	x						x	x								11	
<i>Equus stenonis</i>	x	x		x		x	x	x		x	x	x	x	x										12	
<i>Axis nestii</i>	x	x				x	x	x			x	x	x	x	x									10	
<i>Sus strozzi</i>	x	x				x	x	x			x		x	x	x			x	x					11	
<i>Procamptoceras brivatense</i>	x	x																						2	
<i>Procapreolus</i> sp.																x								1	
<i>Eucladoceros dicranios</i>	x	x												x										3	
<i>Leptobos etruscus</i>	x	x						x			x				x				x					6	
<i>Leptobos merlai-furtivus</i>	x	x																	x					2	
<i>Galgogoral meneghini</i>	x	x																						2	
<i>Canis etruscus</i>	x	x									x		x	x	x				x					7	
<i>Vulpes alopecoides</i>																x								1	
<i>Ursus etruscus</i>	x	x						x							x				x	x	x			7	
<i>Homotherium latidens</i>	x	x					x	x												x				5	
<i>Lynx issiodorensis</i>	x	x						x					x											4	
<i>Megantereon cultridens</i>	x	x				x		x							x	x								6	
<i>Pachycrocuta brevirostris</i>	x	x				x		x							x									5	
<i>Enhydriactis ardea</i>		x																						1	
<i>Chasmaportetes lunensis</i>		x																						1	
<i>Felis lunensis</i>		x																						1	
<i>Panthera gombaszoegensis</i>	x							x					x		x					x				5	
<i>Leptobos</i> sp.			x										x	x					x					4	
<i>Eucladoceros</i> sp.				x		x										x								3	
<i>Leptobos etruscus vel vallisarni</i>						x	x																	2	
<i>Leptobos vallisarni</i>						x		x								x	x		x	x				6	
<i>Eucladoceros dicranios vel ctenoides</i>							x	x			x								x					4	
<i>Galgogoral meneghini</i>							x																	1	
<i>Canis arnensis</i>							x	x						x										3	
<i>Equus stehlini</i>								x											x					2	
<i>Hippopotamus antiquus</i>								x				x		x	x	x			x			x		7	
<i>Xenocyon falconeri</i>								x																1	
<i>Pannonictis nestii</i>								x												x				2	
<i>Stephanorhinus</i> sp.															x									1	
<i>Eucladoceros ctenoides</i>																x								1	
<i>Mammuthus meridionalis vestinus</i>																							x	4	
<i>Stephanorhinus hundsheimensis</i>																			x	x				2	
<i>Axis eurygonos</i>																			x	x	x	x	x	6	
<i>Praemegaceros obscurus</i>																			x	x				2	
<i>Equus</i> sp.																				x				1	
<i>Equus ex gr. bress.-sussebornensis</i>																						x		1	
<i>Bison degiulii</i>																							x	x	2
Total	16	20	3	3	1	9	10	19	2	2	7	2	7	13	12	6	1	9	10	9	3	2	3		

TABLE 3. — Galerian mammal faunas from selected localities in Central Italy. x, local record of each taxon; *, total of local records for each taxon. Abbreviations: **EG**, early Galerian; **MG**, middle Galerian; **LG**, late Galerian; **CC**, Colle Curti; **FR**, Fontana Ranuccio; **Ise**, Isernia; **PG**, Ponte Galeria.

Localities	Monte Peglia	Colle Curti	Ponte Galeria	Vitinia 1	Monte Oliveto	Borgonuovo	Rome-Redicicoli 2	Rome-Ponte Molle 1	Isernia	Cesi	Rome-GRA Km2	Fontana Ranuccio	Cava Nera Molinaro	Rome-Sedia del Diavolo 1	Stazione Predestina (RM)	Total*
Mammal Ages	EG		PG			MG			Ise			LG				
Faunal Units	CC		PG			Ise			FR							
<i>Axis eurygonos</i>	x	x	x	x			x	x							x	6
<i>Xenocyon licanoides</i>		x														1
<i>Canis mosbachensis</i>	x	x							x							3
<i>Homotherium latidens</i>	x									x						2
<i>Ursus sp.</i>	x	x														2
<i>Mammuthus meridionalis vestinus</i>		x														1
<i>Stephanorhinus hundsheimensis</i>	x	x	x				x		x	x						6
<i>Hippopotamus antiquus</i>	x	x			x	x	x	x	x	x						8
<i>Praemegaceros verticornis</i>		x	x		x	x										4
<i>Elephas antiquus</i>		x	x		x	x		x	x			x	x			7
<i>Mammuthus trogontherii</i>			x													1
<i>Equus altidens</i>			x				x									2
<i>Equus sp.</i>			x	x	x					x						3
<i>Megaloceros savini</i>			x													1
<i>Cervus elaphus acoronatus</i>			x	x	x			x	x	x				?		7
"Bos" galerianus			x	?	?											3
<i>Praemegaceros solihacus</i>							x		x	x						3
<i>Bison schoetensacki</i>							x		x	x						3
<i>Stephanorhinus kirchbergensis</i>								x								1
<i>Equus ferus</i>								x				x				3
<i>Sus scrofa</i>								x	x			x				3
<i>Capreolus capreolus</i>								x	x							2
<i>Dama clactoniana</i>								x	x	x	x	x				5
<i>Ursus deningeri</i>								x	x			x				3
<i>Meles meles</i>								x			x					2
<i>Lynx ex gr. issiodorensis</i>								x								1
<i>Panthera fossilis</i>								x	x			?				3
<i>Crocuta crocuta</i>								x								1
<i>Hemitragus bonali</i>									x							1
<i>Bos sp.</i>											x					2
<i>Hyaena prisca</i>											x					1
<i>Equus sussenbornensis</i>						x										1
<i>Hippopotamus amphibius</i>												x	x			2
<i>Cervus elaphus eostephanoceros</i>												x	x			2
<i>Bos primigenius</i>												x				1
<i>Cuon priscus</i>												x				1
<i>Stephanorhinus hemitoechus</i>												x?				1
Total	4	8	11	5	6	4	6	14	13	8	4	11	3	1	1	

TABLE 4. — Early and Middle Aurelian mammal faunas from selected localities in Central Italy. x, local record of each taxon; *, total of local records for each taxon. Abbreviations: EA, early Aurelian; MA, middle Aurelian; TP, Torre in Pietra; Vit, Vitinia.

Localities	Polledrara di Cecanibbio	Torre in Pietra 1	Castel di Guido	Rome-Sedia del Diavolo 2	Malagrotta	Pontecorvo	Riano	Cretone	Bucine	Rome-Ponte Molle 2	Torre in Pietra 2	Vitinia 2	Cerveteri	Casal de Pazzi	Rome-Sedia del Diavolo 3	Monte delle Gioie	Prati Fiscali	Fara Sabina	Campo Verde	Montignoso	Total*	
Mammal Ages	EA										MA											
Faunal Units	TP										Vit											
<i>Elephas antiquus</i>	x	x	x	x	x	x	x		x	x	x	x	x	x	x	x	x	x	x	x	x	19
<i>Stephanorhinus</i> sp.	x					x	x		x			x	x	x								7
<i>Stephanorhinus kirchbergensis</i>			x	x																		2
<i>Equus ferus</i>	x	x	x		x	x					x		x	x	x		x	x	x	x	x	13
<i>Equus sussenbornensis</i>									x													1
<i>Cervus elaphus rianensis</i>	x	x	x		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	19
<i>Capreolus capreolus</i>					x				x	x	x			x						x	x	7
<i>Bos primigenius</i>	x	x	x	x	x				x	x	x	x	x	x	x	x	x	x				16
<i>Canis lupus</i>	x	x	x		x				x	x	x	x		x	x							11
<i>Crocota crocuta</i>									x	x	x			x								5
<i>Stephanorhinus hemitoechus</i>		x		x	x			x			x				x	x	x	x	x	x	x	11
<i>Sus scrofa</i>		x			x	x			x	x	x			x	x				x			10
<i>Megaloceros giganteus</i>		x				x			x											x		4
<i>Vulpes vulpes</i>		x									x	x										4
<i>Ursus spelaeus</i>		x						x														2
<i>Panthera spelaea</i>		x	x																			2
<i>Hippopotamus amphibius</i>			x		x	x				x	x			x	x	x				x	x	10
<i>Canis mosbachensis</i>			x							x				x						x		4
<i>Dama clactoniana</i>					x	x		x	x													4
<i>Meles meles</i>					x					x	x											3
<i>Bison priscus</i>								x	x												x	2
<i>Canis</i> sp.								x														1
<i>Mustela putorius</i>								x														1
<i>Felis silvestris</i>								x													x	2
<i>Mammuthus chosaricus</i>									x											x		2
<i>Dama dama tiberina</i>									x	x	x	x	x	x	x	x	x	x	x	x	x	12
<i>Ursus arctos</i>									x													2
<i>Equus hydruntinus</i>										x					x				x	x		4
<i>Martes martes</i>											x											1
<i>Panthera pardus</i>																		x			x	2
<i>Ursus</i> sp.																			x	x		2
<i>Lynx</i> sp.																					x	1
Total	6	11	9	6	10	7	4	8	14	12	14	7	6	12	10	6	7	9	12	17		

TABLE 5. — Late Aurelian mammal faunas from selected localities in Central Italy. x, local record of each taxon; *, total of local records for each taxon. Abbreviations: **LA**, late Aurelian; **Mel**, Melpignano; **Ing**, Ingarano.

Localities	Grotta dei Moscerini	Saccopastore	Grotta della Cava	Carnello	Valle Radice	Canale Acque Alte	Grotta Orsi Volanti	Grotta Rose Mary	Riparo i Grottoni	Grotta Guattari	Grotta del Fossellone 1	Grotta delle Capre	Grotta S. Agostino 1	Grotta di Monte Cucco	Grotta Cola	Grotta S. Francesco	Grotta S. Agostino 2	Grotta di Gosto	Grotta Breuil	Monte Circeo	Grotta Barbara	Grotta La Fabbrica 1	Cava dei Muracci	Finocchietto	Grotta del Capriolo	Buca della Iena	Buca del Tasso	Grotta all'Onda	Grotta di Equi	Grotta Reali	Total*		
	Mammal Age																LA																
Faunal Units	Mel										Ing																						
<i>Elephas antiquus</i>	x	x	x	x	x	x	x	x	x	x																							7
<i>Mammuthus chosaricus</i>						x																											1
<i>Stephanorhinus hemitoechus</i>	x				x																												2
<i>Stephanorhinus</i> sp.	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	12	
<i>Equus ferus</i>			x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	16	
<i>Equus hydruntinus</i>	x	x	x	x	x	x	x	x								x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	9		
<i>Equus</i> sp.	x	x			x						x							x														5	
<i>Hippopotamus amphibius</i>	x	x	x		x					x																						5	
<i>Sus scrofa</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	20	
<i>Capreolus capreolus</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	23	
<i>Cervus elaphus elaphus</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	28	
<i>Dama dama dama</i>	x	x			x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	16	
<i>Megaloceros giganteus</i>										x																	x						2
<i>Bos primigenius</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	25	
<i>Bison priscus</i>											x																						1
<i>Canis lupus</i>		x			x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	20	
<i>Vulpes vulpes</i>			x	x		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	19	
<i>Ursus arctos</i>		x			x				x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	9	
<i>Ursus spelaeus</i>			x	x	x			x					x	x							x					x	x	x	x	x	x	12	
<i>Ursus</i> sp.	x	x									x	x							x													6	
<i>Mustela putorius</i>									x											x						x	x	x	x	x	x	5	
<i>Meles meles</i>						x										x										x	x	x				5	
<i>Felis silvestris</i>												x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	10	
<i>Lynx lynx</i>			x	x												x	x								x							4	
<i>Panthera pardus</i>		x	x	x			x					x				x									x	x	x	x	x	x	x	11	
<i>Crocota crocuta</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	15	
<i>Capra ibex</i>			x	x					x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	13	
<i>Martes martes</i>			x	x			x					x	x								x						x	x	x				7
<i>Panthera spelaea</i>		x	x	x			x																	x			x						7
<i>Rupicapra rupicapra</i>							x					x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	8	
<i>Mustela nivalis</i>								x						x																	x		3
<i>Coelodonta antiquitatis</i>																																	1
<i>Mammuthus primigenius</i>																											x						1
<i>Cuon alpinus</i>																											x	x					2
<i>Mustela erminea</i>														x																	x		1
Total	107	12	16	15	13	11	9	10	18	11	8	13	7	9	4	16	12	15	1	10	10	7	9	9	19	15	14	18	7				

TABLE 6. — Latest Aurelian mammal faunas from selected localities in Central Italy. x, local record of each taxon; *, total of local records for each taxon. Abbreviations: **Aur**, Aurelian.

Localities	Grotta del Fossellone 2	Grotta La Fabrica 2	Buca dei Ladri	Talamone-Grotta di Golino	Grotta C. Tronci	Rome-Tor Vergata	Grotta La Fabrica 3	Riparo Maurizio	Montopoli-ponte sfondato	Palidoro	Valle Ottara	Grotta A. Graziani	Grotta di C. Felice	Riparo Biedano	Grotta di Ortucchio	Riparo Salvini	Grotta Maritza	Riparo Venere dei Marsi	Valle Arcione	Vado all'Arancio	Grotta del Ponte Nero	Grotta della Campana	LI-Podere Greppi Cupi	Riparo Piastricoli	Riparo Fredian	Cava Romita	Grotta Continenza	Grotta Polesini	Total*	
Mammal Age	Aur																													
Isotopic Stage	2																													
<i>Equus ferus</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	13
<i>Equus hydruntinus</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	19
<i>Sus scrofa</i>	x			x	x				x			x		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	16
<i>Capreolus capreolus</i>	x	x	x	x				x	x	x					x	x				x	x	x		x	x	x	x	x	x	17
<i>Cervus elaphus elaphus</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	27
<i>Dama dama dama</i>	x	x																												2
<i>Bos primigenius</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	26
<i>Capra ibex</i>	x			x	x				x	x	x	x	x	x	x	x	x				x	x	x	x	x	x	x	x	x	19
<i>Rupicapra rupicapra</i>	x	x									x	x	x	x	x	x						x		x	x	x	x	x	x	14
<i>Canis lupus</i>	x	x							x		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	15
<i>Cuon alpinus</i>																														1
<i>Vulpes vulpes</i>	x		x	x					x		x	x	x	x	x	x														12
<i>Ursus arctos</i>								x																						4
<i>Ursus sp.</i>																														1
<i>Ursus spelaeus</i>				x																										1
<i>Martes martes</i>			x									x					x				x	x	x					x	x	7
<i>Mustela erminea</i>															x															1
<i>Mustela nivalis</i>															x	x	x												x	4
<i>Mustela putorius</i>					x												x													2
<i>Meles meles</i>				x					x			x					x				x	x						x	x	8
<i>Gulo gulo</i>																														2
<i>Felis silvestris</i>					x										x	x								x	x			x	x	7
<i>Lynx lynx</i>					x												x				x								x	4
<i>Panthera spelaea</i>										x																				2
<i>Crocuta crocuta</i>	x	x		x			x																							4
Total	12	9	7	13	6	2	5	6	2	11	3	9	10	4	10	6	16	9	4	10	7	8	4	9	13	5	12	17		

TABLE 7. — Database and turnover index for large mammal species. Abbreviations: **FO**, number of first occurrences; **LO**, number of last occurrences. Turnover Indexes formulas: **TI**, = %FO+%LO/2; running mean formulas: **rm**, = N-(FO+LO/2); percentage of FO formulas: %**FO**, = FO/Running mean*100; percentage of LO formulas: %**LO**, = LO/running mean*100.

	No. species	FO	LO	Running mean	%FO	%LO	Turnover index
Italy							
Holocene/OIS2	26	0	7	22.5	0	31.11	15.55
OIS2/Ingarano	31	0	5	28.5	0	17.54	8.77
Ingarano/Melpignano	33	3	3	30	10	10	10
Melpignano/Vitinia	36	2	5	32.5	6.15	15.38	10.76
Vitinia/Torre in Pietra	27	5	2	23.5	21.27	8.51	14.89
Torre in Pietra/Fontana Ranuccio	29	4	7	23.5	17.02	29.78	23.4
Fontana Ranuccio/Isernia	34	5	9	27	18.51	33.33	25.92
Isernia/Ponte Galeria	31	10	2	25	40	8	24
Ponte Galeria/Slivia	18	4	0	16	25	0	12.5
Slivia/Colle Curti	16	2	3	13.5	14.81	22.22	18.51
Ponte Galeria/Colle Curti	27	11	6	18.5	59.46	32.43	45.94
Colle Curti/Pirro	22	2	6	18	11.11	33.33	22.22
Pirro/Farneta	29	5	9	22	22.72	40.9	31.81
Farneta/Tasso	32	6	8	25	24	32	28
Tasso/Olivola	31	10	5	23.5	42.53	21.27	31.9
Olivola/Costa S. Giacomo	26	6	6	20	30	30	30
Costa S. Giacomo/Montopoli	27	10	9	17.5	57.14	51.42	54.28
Montopoli/Triversa	24	8	5	17.5	45.71	28.57	37.14
Central Italy							
Holocene/OIS2	24	0	7	20.5	0	34.14	17.07
OIS2/Ingarano	29	1	5	26	3.84	19.23	11.53
Ingarano/Melpignano	33	4	5	28.5	14.03	17.54	15.78
Melpignano/Vitinia	34	8	5	27.5	29.09	18.18	23.63
Vitinia/Torre in Pietra	29	7	3	24	29.16	12.5	20.83
Torre in Pietra/Fontana Ranuccio	26	8	5	19.5	41.02	25.64	33.33
Fontana Ranuccio/Isernia	29	4	11	21.5	18.6	51.16	34.88
Isernia/Ponte Galeria	27	12	2	20	60	10	35
Ponte Galeria/Colle Curti	17	8	2	12	66.66	16.66	41.66
Colle Curti/Pirro	10	3	1	8	37.5	12.5	25
Pirro/Farneta	18	1	11	12	8.33	91.66	50
Farneta/Tasso	28	5	11	20	25	55	40
Tasso/Olivola	28	5	5	23	21.74	21.74	21.74
Olivola/Costa S. Giacomo	34	15	11	21	71.42	52.38	61.9
Costa S. Giacomo/Montopoli	25	11	5	17	64.7	29.41	47.05
Montopoli/Triversa	15	12	2	8	150	25	87.5