BIOCHRONOLOGY OF TERRESTRIAL MAMMALS AND QUATERNARY SUBDIVISIONS: A CASE STUDY OF LARGE MAMMALS FROM THE ITALIAN PENINSULA

Maria Rita Palombo

Dipartimento Scienze della Terra Università La Sapienza, CNR, Istituto di Geologia Ambientale e Geoingegneria,
P.le Aldo Moro, 5 00185 Roma, Italy. E-mail: mariarita.palombo@uniroma1.it

ABSTRACT: Palombo M.R., *Biochronology of terrestrial mammals and Quaternary subdivisions: a case study of large mammals from the Italian peninsula* (IT ISSN 0394-3356, 2009).
Defining and subdividing the Quaternary on the basis of the mammalian fossil record from the continental realm is not a simple task due to the low degree of succession continuity and the scattered palaeontological evidence. Moreover, even if the approaches to the Quaternary are basically interdisciplinary and may combine many different chronological scales, establishing correlations between biochronology, biostratigraphy, chronostratigraphy, climatostratigraphy, and composite regional stratigraphy can often be very problematical. As far as biochronology is concerned, the marked geological, environmental and climatic diversity affecting different continental regions makes a correlation based on biological events difficult. Indeed, "biochronological units" represent a time span during which faunas have a degree of taxonomic homogeneity and the corresponding "faunal complexes" have to be regarded as non- overlapping and "ecologically adjusted groups of animals with specific geographic limits and chronological range" (TEDFORD, 1970). Nevertheless, the stratigraphic lowest and highest occurrences of fossil remains (stratigraphic datum) within a given geographical area do not necessarily correspond to their actual first/last appearances (palaeobiological events) in time. This is due to diachroneity in palaeobiological events (i.e. local first and last appearances are strictly linked to dispersal, and the physical and biotic factors causing local evolution and extinctions) coupled with discontinuity in the continental sedimentary record, the rarity of deposits formed in a regime of virtually continuous sedimentation, the presence of important ecological barriers (that prevent some taxa from dispersing), environmental conditions (that affect the structure of palaeocommunities), and taphonomic and sampling biases. As a result, ongoing research, continuously yielding new data, make chronological frameworks thus far outlined, even if recent, open to significant improvements, and causing biochrons to be updated. This fact prevents any detailed biochronological framework from having widespread geographical significance. Thus, only higher ranking biochronological units (Land Mammal Ages, LMAs) - whose separation is based on palaeobiological events which have a wide territorial significance - could be useful for chronological correlations. Nonetheless, the transition between successive LMAs does not always correspond to the boundaries separating marine Series or Stages. For instance, the Villafranchian LMA approximately began with the Late Pliocene (Piacentian) and the transition from the early to the middle Villafranchian LMA happened around the Pliocene/Pleistocene (Piacentian/Gelasian) boundary, whereas the transition to the late Villafranchian took place during the latest Gelasian, and those from the Villafranchian to Galerian LMA and from the Galerian to Aurelian LMA respectively predated the beginning of the Middle and Late Pleistocene.

RIASSUNTO: *Palombo M.R.,* Biocronologia dei mammiferi terrestri e suddivisioni del Quaternario: l'esempio delle faune a grandi mammiferi della penisola italiana. *(IT ISSN 0394-3356, 2009).*
Definire e suddividere il Quaternario sulla base del record fossile dei mammiferi continentali non è un compito facile ed anche se gli approcci al Quaternario sono fondamentalmente interdisciplinari e tendono a combinare diverse scale cronologiche, stabilire correlazioni tra biocronologia, biostratigrafia, cronostratigrafia, climatostratigrafia, e stratigrafia regionale è spesso problematico. Sebbene le unità basate su eventi biologici e climatici siano di largo uso nel Quaternario continentale, il loro status non è stato formalmente definito e questo alimenta dubbi nell'approccio metodologico e confusione tra teoria (dato Paleobiologico) ed operatività (dato stratigrafico). Dal punto di vista teorico, le " unità biochronologiche" rappresentano un lasso di tempo durante il quale le faune locali hanno un certo grado di omogeneità tassonomica ed i "complessi faunistici" che caratterizzano le singole unità devono essere considerati "non-overlapping and ecologically adjusted groups of animals with specific geographic limits and chronological range" (TEDFORD, 1970). Tuttavia, l'evidenza stratigrafica della prima e ultima presenza di un fossile nelle successioni affioranti in una determinata area geografica (dato stratigrafico) non corrisponde necessariamente all'effettiva prima e ultima comparsa di quel taxon nel tempo (evento paleobiologico). Ciò si deve alla diacronicità degli eventi paleobiologici (ad esempio gli eventi locali di comparsa e scomparsa sono strettamente legati rispettivamente alla dispersione ed ai fattori fisici e biotici che regolano diffusione ed estinzione), alla discontinuità del record sedimentario continentale, alla rarità di depositi formati in regime di sedimentazione continua, alla presenza di barriere ecologiche (che limita o impedisce la dispersione di alcuni taxa in certuni territori), alle condizioni ambientali locali (che influenzano la struttura delle Paleocomunita), a problemi tafonomici e di campionamento. Questi limiti rendono instabili schemi biocronologici dettagliati basati su un record fossile regionale, in quanto essi sono fortemente dipendenti dal progredire delle conoscenze sul campo. Fin dalla prima introduzione delle unità faunistiche (FUs) (Azzaroli 1977), sulle quale si fonda la biocronologia dei grandi mammiferi della penisola italiana, il progredire delle ricerche e la scoperta di nuove faune ha portato sia alla ridifinizione e/o eliminazionedi alcune FUs sia alla creazione di nuove. Ne consegue che, proprio in funzione della possibilità di discriminare singoli bioeventi, ogni schema biocronologico delle faune italiane risulta quanto più dettagliato tanto meno stabile nel tempo, nonché difficilmente confrontabile con gli schemi proposti per l'Europa continentale. In realtà, l'utilizzo di unità biochronologiche di più alto rango (Land Mammal Age, LMA) - la cui separazione è basata su eventi paleobiologici validi a grande scala e cambi di struttura dei complessi faunistici – meglio si presta a correlazioni su vasta scala. La transizione tra successive LMA, tuttavia, non sempre corrisponde ai limiti che separano Serie e Stadi. Per esempio, il Villafranchiano inizia con il Pliocene superiore (Piacenziano), la transizione al Villafranchiano medio potrebbe coincidere grosso modo con il limite Pliocene/Pleistocene (Piacenziano / Gelasiano), ma il passaggio al Villafranchiano superiore avviene nel tardo Gelasiano, e le transizioni Villafranchiano/Galeriano e Galeriano/Aureliano precedono, rispettivamente, l'inizio del Pleistocene medio e superiore.

Key words: Biochronology, Biostratigraphy, Plio-Pleistocene, Large Mammals, Itay.

Parole chiave: Biocronologia, Biostratigrafia, Plio-Pleistocene, grandi Mammiferi, Italia.

1. INTRODUCTION

Defining and subdividing the Quaternary on the basis of the mammalian fossil record from the continental realm is not a simple task due to the low degree of succession continuity and the scattered palaeontological evidence. Moreover, even if the approaches to the Quaternary are basically interdisciplinary and can combine many different chronological scales, establishing correlations between biochronological, chronostratigraphical, climatostratigraphical frames and composite regional stratigraphy can be problematical (concerning Italy, see e.g. DE GIULI et al., 1983; RAVAZZI, 2003; PALOMBO, 2004a; PALOMBO & SARDELLA, 2007 and references therein).

With regard to terrestrial fauna, especially mammals, diachroneity in palaeobiological events coupled with discontinuity in the continental sedimentary record, the rarity of deposits formed in a regime of virtually continuous sedimentation, the presence of important ecological barriers (that prevent some taxa from dispersing), environmental conditions (that affect the structure of palaeocommunities), and taphonomical and sampling biases make the definition of isochronous boundaries, maybe of boundaries themselves, problematical. Therefore, any biochronological framework is predisposed to change depending on new discoveries.

During the latter half of the last century, study on the terrestrial mammals of the Italian peninsula was developed mainly on the basis of large-sized mammalian taxa. The Italian mammal biochronological framework builds on the pioneering work of Azzaroli (AZZAROLI, 1977, 1982), who first introduced the "Faunal units"(FU's) as "biochrons", defined on the basis of all the species from selected local faunal assemblages (LFA's). Like Land Mammal Ages (LMAs) which are the primary unit of North American vertebrate chronology (see TEAFORD,1970; LINDSAY & TEDFORD, 1990), FU's represent and are defined by typical associations of mammalian taxa (biological entities), each living in non-overlapping slices of time. As suggested by Lindsay (2003, pg. 222) for LMA's, FU's could be defined as "a relatively short interval of geological time that can be recognized and distinguished from earlier and later such units (in a given region or province) by a characteristic assemblage of mammals". Although sometimes criticised (e.g. GUERIN, 1982, 1990), FU's are general concepts, especially used by the Italian scientific community. Since the time of the FU's introduction, Italian palaeontologists have proposed new or revised some FU's/LMA's (see e.g. DE GIULI, et al. 1983, TORRE, 1987; AZZAROLI et al., 1988; SALA, et al., 1992; TORRE, et al. 1992; CALOI & PALOMBO, 1990, 1996; GLIOZZI et al., 1997, PETRONIO & SARDELLA, 1999; PALOMBO et al., 2004; PALOMBO, 2004a, 2007a; MASINI & SALA, 2007; PETRONIO et al.,.2007) (Table 1). The introduction of new biochrons mainly depends on acquiring new data and discovering new fossiliferous assemblages, which makes possible, by means of ever more detailed biostratigraphical settings, increasingly accurate discrimination between bioevents.

This paper's aim is to outline the pricipal problems related to biostratigraphy/biochronology of large Italian mammals, and to update the previous biochronological schemes according to the most recent discoveries (Table 2.3).

2. ABOUT CHRONOSTRATIGRAPHY, BIOCHRO-NOLOGY, BIOSTRATIGRAPHY AND RELATED ITEMS: A SHORT SKETCH

As stated by Lindsay (2003) chronostratigraphy - the dominant method applied in the oceanographic-marine realm - and biochronology - the dominant method for the terrestrial realm - are the prime conceptual methods for relating biological events to the geological time scale. The chronostratigraphical concept was introduced by SCHENCK & MULLER (1941), who proposed a new ''chronostratigraphical'' hierarchy (System, Series, and Stage) for the stratigraphical representation of equivalent chronological intervals (Period, Epoch, and Age). Recently, LINDSAY (2003, pg. 227) defined chronostratigraphy as: "the sequential ordering of geologic events, using biostratigraphic, isotopic-radiometric, and paleomagnetic data". The concept of biochronology dates back the beginning of the 20th century, when WILLIAMS (1901) defined a "biochron" as the absolute time extent of a peculiar faunal or vegetal association. Later, TEICHERT (1958) described biochronology as ''the dating of geological events by biostratigraphical methods'', but did not characterise biochronological terms, such as ''biochronological unit'', and concepts relative to the biostratigraphical ones. Due to that loose definition and to its ambiguous application, biochronology has never been discussed in any stratigraphical code (LINDSAY, 2003). Up to the present day, the operation of organising geological time on the basis of evidence provided by continental mammal faunas has continued to be a field plagued by interpretative and semantic confusion. BERGGREN & VAN COUVERING (1978, pag. 39) tried to avoid ambiguity defining biochronology as ''the organization of geological time according to the irreversible process of evolution in the organic continuum''. Subsequently, LINDSAY (2003, pag. 227) defined biochronology as the "sequential ordering of biologic (and geologic) events, using morphologic differences that result from organic evolution (when applied to Earth history)".

On the other hand, it is widely known that the discipline of biostratigraphy establishes the stratigraphical ranges of the taxa remains within superimposed sections, and verifies the relative age of rocks using the fossil data. Biostratigraphy is the element of stratigraphy which focuses on "the distribution of fossils in the stratigraphical record and the organization of strata into units on the basis of their contained fossils" (SALVADOR, 1994, pag.55). But as claimed by SALVADOR (1994, pag.55) biostratigraphical units, including biozones, "vary greatly in thickness and geographic extent. ......The time they represent may likewise vary widely". To avoid this issue, WALSH (1998) defined the biochronostratigraphical units as "the sets of rock formed during biochrons, without reference to any particular stratigraphic section". As a result, a biochronological unit should be characterised and defined as a span of time defined by biological evidences (palaeobiological datum), while a biostratigraphical unit as a body of rock strata defined by its fossil content (stratigraphical datum) (SCHOCH, 1989; SALVADOR, 1994).

Table 1 - Comparison among selected biochronological schemes proposed for the Italian mammalian faunas.

2.1. In search of a stable biochronological frame for the terrestrial large mammals: utopia or feasible undertaking?

As defined above, "biochronological units" represent a time span during which faunas are assumed to be characterised by taxonomical homogeneity and should be regarded as non- overlapping and an "ecologically adjusted group of animals within specific geographic limits and chronologic range" (TEDFORD, 1970). First/last appearance bioevents (palaeobiological events on which biochronology is based) have been the principal bases for establishing the chronological setting of continental mammalian faunas. However, the marked geological, environmental and climatic diversity affecting different continental regions, as well as the discontinuity in the continental sedimentary record, the rarity of deposits formed in a regime of virtually continuous sedimentation, the diachroneity in palaeobiological events (i.e. local first and last appearances are strictly linked respectively to dispersal, and the physical and biotical factors causing extinctions), taphonomical and sampling biases are responsible for the fact that the stratigraphical order of the highest and lowest occurrences (stratigraphical datum) of fossil remains of some taxa within a given geographical area, does not necessarily reflect the temporal order of the actual first/last appearances (palaeobiological events) of each taxon in time. Indeed, a stratigraphical discontinuity within a sedimentary succession (whether due to erosional phases or sedimentation lacking) corresponds to a time span during which palaeobiological events do not yield a stratigraphical record. Moreover, fossil remains of taxa characterising a given biochronological unit do not necessarily appear in each section because they were absent from the depositional environment for ecological or taphonomical factors. Therefore, the time range of a paleobiological entity (either in general or in a given geographical area) cannot be unquestionably established by its fossil evidence. The lowest and highest stratigraphical records of a taxon, respectively correspond to the time "ante" or "post quem" when it actually originated and became extinct (PALOMBO 2004a). Accordingly, it should be appropriate to discriminate taxon longevity from time slice of its fossil record, e.g. first/last historical appearance bioevents (FHA/LHA = First/Last Historical Appearance) from "known data" of lowest and highest occurrences in a local stratigraphical section (LISDk/HISDk = local Lowest/Highest known Stratigraphical Datum) (WALSH, 1998; PALOMBO & SARDELLA, 2007). On the other hand, mammalian biochronology is actually founded on fossil records available in the continental rocks, FHA/LHA bioevents can only be inferred from the lowest/highest occurrences of fossil remains in fossiliferous levels, maybe based on more than one continental stratigraphical section. Hence, new discoveries may substantially change the chronological extent of already defined biochrons. Indeed, the finding of a/some taxon/a (whose LHA/LHA were already regarded as markers of a biochrons) in significantly older/younger extends the theoretical time range of such a biochron, without changing its theoretical definition. As a result, ongoing research, continuously providing new data, makes chronological frameworks thus far outlined, even if recent, open to significant improvements. Some biochrons, consequently, will require revisions and updated definitions.

3. FAUNAL TURNOVERS, BIOCHRONS AND QUATERNARY SUBDIVISIONS

During the Pliocene and Pleistocene a series of climatic cycles caused latitudinal displacements of vegetation and biomes in Europe and exerted great influence on dispersal and dispersion of mammalian species. As a result, the composition of regional faunas changed because of origination/ extinction and dispersal bioevents. On the Italian peninsula, climatic changes were a driving factor, at least as far as the two most important detectable faunal renewals are concerned: the Early to Middle Villafranchian LMA (Piacentian to Gelasian, ~2.7–2.5 Ma) and Early to Middle Galerian LMA, transition (latest Early Pleistocene, ~1.1–0.8 Ma). Faunas changed also at the end of the Gelasian (Middle to Late Villafranchian transition) and at the end of the Middle Pleistocene (Galerian to Aurelian transition), but to a lesser degree (PALOMBO, 2007b and references therein).

3.1 The beginning of the Villafranchian and the warning signs of the already called "Glacial Pliocene"

The list of early Villafranchian taxa have been established on a number of LFA's from Piedmont (several localities in the Villafranca d'Asti area) and central Italy (e.g. Lower and Upper Valdarno, Arcille, Spoleto). Palaeomagnetic data at Fornace R.D.B. (Villafranca d'Asti) (LINDSAY et al., 1980, 1995) as well paleomagnetic calibration of the long sedimentary sequence outcropping at Santa Barbara quarry (lignitic lacustrine silty clays and sands, Meleto clays of Castelnuovo dei Sabbioni Lower Synthem of the Upper Valdarno basin) (TORRE et al., 1996; BERTINI & ROION, 1997; NAPOLEONE et al., 2003; GHINASSI et al., 2004) illustrate that, at about 3.2 Ma, the faunal association regarded as typical of the early Villafranchian was already present on the Italian peninsula.

The early Villafranchian LMA (Triversa FU) retains subtropical affinities typical of Ruscinian mammals, which lived during the Early Pliocene, the most recent interval with a climate definitively warmer than today. Pachyderms, middle sized Artiodactyla, and Perrissodactyla, mainly browsers or mixed-feeders inhabiting dense or clear forest, were still present along with arboreal/scansorial viverrids and arboreal omnivores, such as *Mesopithecus monspessulanus, Parailurus hungaricus* and *Ursus minimus*. On the other hand, the appearance of some taxa, such as *Leptobos stenometopon* and *Stephanorhinus jeanvireti* (= *Stephanorhinus elatus*) (Table 3), perhaps more linked to wooded parkland environment, testified to a change in faunal structure which can be correlated with the climatic cooling, which occurred at about 3.2/3.1 (KM2 isotopic stage) (Table 2).

3.2 Early to Middle Villafranchian and the Piacentian to Gelasian transition

The following Montopoli FU is based on rich fauna from a site near Montopoli (Lower Valdarno, Tuscany),

Table 2 - Integrated chronological scheme for the Middle Pliocene to Late Pleistocene large mammalian record of the Italian peninsula.
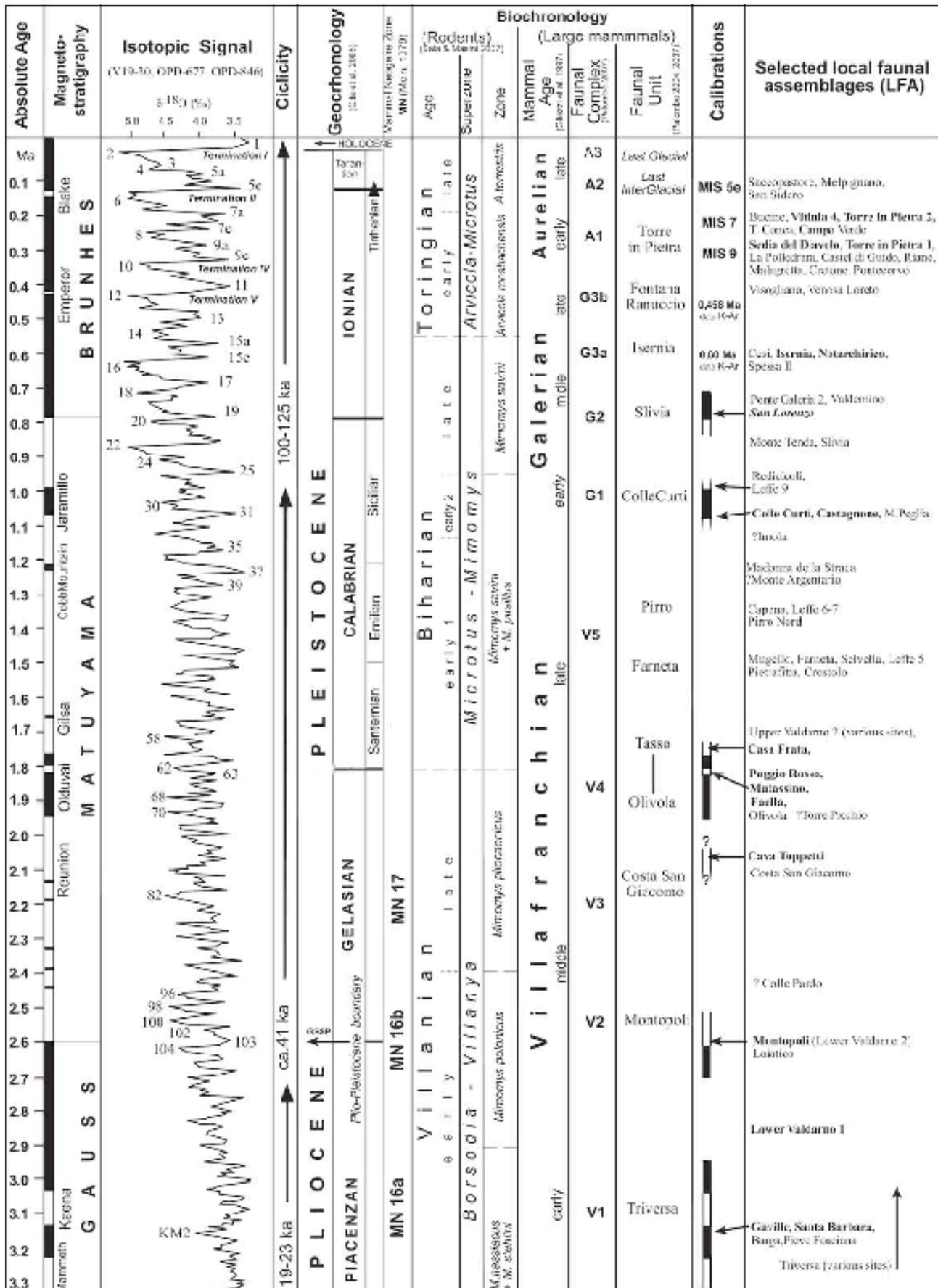
found in a fossiliferous level at the top of a shallow-water marine sequence of Late Pliocene age (BENVENUTI *et al*., 1995), calibrated with the Gauss/ Matuyama transition (LINDSAY *et al.,* 1980). The Montopoli FU should correspond to the MN16b zone and was traditionally included in the Early Villafranchian LMA (Table 1), but the marked faunal turnover characterising the transition from the Triversa FU to the Montopoli FU recommends regarding it as the basal unit of the Middle Villafranchian (Caloi & Palombo 1990, 1996). The faunal renewal from Triversa to the Montopoli FU can be regarded as a true turnover phase, due to the high percentage of last and new appearances, but also to the important structural changes in the faunal complexes, in both the herbivore and carnivore guilds. This is consistent with the significant global changes characterising the Piacentian to Gelasian transition (actually the beginning of the Quaternary as proposed by several authors, see e.g. BOWEN & GIBBARD, 2007), with the permanent ice-sheet growth in the Northern Hemisphere, the first major influx of ice-rafted debris in the middle latitudes of the North Atlantic, the onset of extensive loess deposition in China around the Gauss/Matuyama boundary (marine isotopic stage, MIS, 104 to 100) (see inter alios RUDDIMAN *et al*., 1989; DING *et al.*, 1997; SHACKLETON, 1997; PARTRIDGE, 1997a, b; RIO *et al*. 1998; BOWEN & GIBBARD, 2007 and recently ratified by the International Commission on Stratigraphy, GIBBARD & HEAD, 2009), the profound changes in Eurasian flora assemblages (see inter alios ZAGWIJN, 1974; GRICHUK, 1997; SUC *et al*., 1997). Bioevents behind this faunal change (e.g. the so-called "elephant-*Equus* event", Lindsay *et al.,* 1980) likely occurred close to the Piacentian- Gelasian boundary, driven by climatic cooling, as well as by the effects of changes in the Earth climate system: 19-23 ka cycles were superseded progressively by a 41-ka rhythm (orbital obliquity periodicity) accompanied by moderately increased amplitude climatic oscillations. The resulting increase in aridity and more intense seasonality triggered vegetation to reconstruct (SUC *et al.*, 1995, and references in Bertini, 2003) and caused the disappearance of most forest-dwelling taxa, especially small carnivores and arboreal-scansorial taxa, whereas new large grazers (the horse *Equus livenzovensis*), mixed feeders (a primitive *Mammuthus meridionalis,* the medium-size *Gazella borbonica*) or even browsers (the deer *Eucladoceros falconeri*) appeared (Table 3).

The taxonomical composition of the Montopoli FU resulted primarily from the dispersal, mostly from Eastern Europe, of large to medium-sized herbivores, while evolutionary substitutions within surviving phyletic lineages were rather negligible. The faunal change indicates that forests gradually gave way to more open environments (including *Artemisia* steppe), alternating with warm temperate deciduous forests (see Bertini, 2003). Indeed, from an ecological point of view, the Triversa faunal complex, which had a relatively high frequency of frugivores, developed in environments rather similar to those of modern forests, whereas the structure of the Montopoli faunal complex shows some affinities with those of modern bush-woodland (PALOMBO & GIOVINAZZO, 2006, PALOMBO 2007b). Moreover, this event can be considered as the beginning of a dispersal phase leading to a progressive

increase in standing richness during the subsequent Pliocene and up to the beginning of the Early Pleistocene.

A temperate interlude occurred between 2.5 and 1.8 Ma; during this phase the Mediterranean climate was established permanently in southwestern Europe. A progressive faunal renewal took place, and some dispersal/origination bioevents led to a moderate faunal structural reconstruction of late middle Villafranchian fauna. Two FU's have been proposed as characterising this time slice, the "*Saint Vallier"* and the Costa San Giacomo FU (Table 1), but the Italian "*Saint Vallier"* FU is loosely defined as being based on sporadic finds of taxa that also occur in the LFA's assigned to the Costa San Giacomo FU. Accordingly, the author is inclined to consider the Italian late middle Villafranchian LFA'S as belonging to only one FU. The "Costa San Giacomo" name is here retained despite the priority of *"Saint Vallier"*. This is because of the rich fossil record of the corresponding LFA (Costa San Giacomo, Anagni, Latium), as well to stress the significance of the appearance on the Italian peninsula of a wolf-like canid closely related to *Canis etruscus* (a primitive representative of this phyletic lineage might be already present in the early Villafranchian Vialette LFA, LACOMBAT *et al.*, 2008). As here redefined, the Italian Costa San Giacomo FU should roughly correspond to the MN 17"zone". The faunal composition is similar to that of the preceding unit as regards the presence of taxa such as *"Pseudodama" lyra, Eucladoceros tegulensis, Gazella borbonica*, or long-surviving taxa such as the cheetah, *Acinonyx pardinensis*, the hunting hyaena *Chasmaporthetes lunensis* and the proboscidean *A. arvernensis,* but renewed because of the first appearance, among others, of the middle-sized horse *Equus stenoni*s, the goat *Gallogoral meneghini,* and the spiral horned antelope *Gazellospira torticornis,* all parkland dwellers, as well the large-sized and slender legged boar *Sus strozzii.*

The presence in the Costa San Giacomo of *Canis* aff. *C etruscus* bears witness that the so-called "wolf-event" (AZZAROLI 1983, 1995) was already in progress. The carnivore guild renewal was a gradual phenomenon (SARDELLA & PALOMBO 2007, PALOMBO *et al*., 2008), which developed throughout the latest Gelasian and the earliest Calabrian and involved several large and middle-sized carnivores, such as the powerful scavenger, *Pachycrocuta brevirostris*, the jaguar-like *Panthera gombaszoegensis (= Panthera onca toscana* according to HEMMER *et all.,* 2003)*,* the cooperative foraging canid, *Lycaon (Xenocyon) falconeri,* as well the coyote-like (but see OLIVE, 2006) *Canis arnensis* (PALOMBO *et al.,* 2008 and references therein)*.*

3.3 The Late Villafranchian and the Gelasian-Calabrian boundary

The latest Gelasian faunal renewal involved both carnivores and herbivores: most Pliocene and Early Gelasian species disappeared, particularly among herbivores, and new carnivores and herbivores progressively appeared (Table 3). The renewal from the middle to late Villafranchian LMA, should be regarded as a dispersal phase (more than an actual turnover), which developed before and after the Gelasian-Calabrian boundary, and came to an end during the earliest Early

Table 3 – Biochronology of selected large mammals of Italian peninsula from the Middle Pliocene to the Late Pleistocene.

Calabrian, (Palombo, 2004b, 2007a, b). The dispersal phase primarily involved carnivores, since among new taxa none belong to species which evolved *in loco,* whereas new appearances among herbivores were principally linked to the emergence of new species within pre-existing phyletic lineages (e.g. *Mammuthus, Equus, Eucladoceros, "Pseudodama"* and large bovids of subgenus *Leptobos*), and subordinately, to immigration of large ruminants, mainly mixed feeders (e.g. *Procamptoceras* and *Praevibos*). These faunal changes indicate that forests or woodlands gradually gave way to more open environments (including *Artemisia* steppe), but alternating with warm-temperate deciduous forests. The gradual faunal reconstruction from the latest Gelasian to Early Calabrian took form within an interval of climatic transition, and was possibly driven both by climatic worsening (moderate average cooling MIS 70 to58), and modification of internal competitive dynamics, the latter depending on the disappearances of some pre-existing key taxa and ensuing availability of ecological niches (Palombo, 2007b).

After Azzaroli (1977) the late Villafranchian, at this time considered as coincident with the early Pleistocene (*sensu* Aguirre & Pasini, 1985), would include three FU's: Olivola, T and F (Table 1). Subsequently, a more recent, fourth FU, Pirro was added, and the end of the late Villafranchian was dropped before the Jaramillo subchron (Table 1). LFA's assigned to the Olivola and Tasso FU's are well-known from the Upper Valdarno Basin, where fossil-bearing sediments of two stratigraphically superimposed units are exposed (De Giuli & Masini, 1987; Torre, 1987; Azzaroli *et al.*, 1988). Magnetostratigraphy of these fossiliferous stratigraphical successions provides chronological constraints for Olivola plus the Tasso FU: in the Upper Valdarno area, LFA's assigned to the Tasso FU have been correlated to the top of the Olduvai subchron (Napoleone *et al.*, 2003), which is around the GSSP of the Gelasian-Calabrian boundary (La Vrica Section; Aguirre & Pasini, 1985), whereas LFA's of the Olivola FU (e.g. Matassino and Poggio Rosso LFA's) are "inferred as pre-Olduvaian, not younger than 2.0 Ma." (Napoleone *et al.,* 2003, pag. 308).

The tructure of the faunal complexes of the Olivola and Tasso FU's are not very dissimilar, the latter being different essentially for the appearance, among others, of *Lycaon (Xenocyon) falconeri* (already present in the latest Pliocene Spanish fauna of Fonelas P-1, Garrido, 2008), *Equus stehlini* (= *Equus senezensis stehlini,* according to Alberdi *et al.*, 1998) and the stout bovid *Leptobos vallisarni. Praeovibos* is also recorded in the Casa Frata LFA, whereas *Gallogoral, Gazellospira* and *Procamptoceras were* not reported (Table 3). The occurrence of *Hippopotamus antiquus* in the Tasso FU is doubtful, since hippopotamuses from Valdarno (already ascribed to the Tasso FU), was probably retrieved from fossiliferous layers younger than those of the Montervarchi succession (Napoleone *et al.*, 2003). On the other hand, the occurrence in the same stratigraphical layer of *H. antiquus* and *Leptobos* aff. *furtivus* at Piano dei Cavalieri (Rieti basin, Latium) (Masini 1989, Gentili & Masini, 2005), needs to be confirmed (see Segre Naldini & Valli and references therein). Accordingly, faunas assigned to Olivola and Tasso FU's seem to be part of the same, progressive faunal renewal, and the hypothesis that they could represent a single FU cannot be ruled out.

3.4 The end of the Villafranchian LMA and the dawn of the Galerian LMA

During the subsequent Early Pleistocene (Farneta, Pirro and Colle Curti FU's) (Table 2) an important renewal of faunas occurred: most of the typical Villafranchian taxa disappeared or became rare while scattered bioevents led to the appearance of new species, either newcomers or ones evolved from preexisting taxa (Table 3). The previously mentioned increase in diversity throughout the early late Villafranchian (mainly via migrations and dispersal events) had possibly altered the palaeocommunity equilibria, and climate changes possibly removed keystone species causing new intra- and inter-guild dynamics, leading mammalian communities to significantly reconstruct (Palombo, 2007b). This is the reason why, despite the progressive appearance of new species (most of which will survive in the early Middle Pleistocene), last appearances prevailed, leading to a progressive reduction in diversity from Farneta to Colle Curti FU's (Table 3).

3.4.1 Farneta and Pirro FU's

Differences in taxonomical composition and structure between Tasso and the following Farneta FU are mainly related to changes in the herbivore guild and mirror the spread of open environments due to the decrease in average temperature, along with the increase in dryness (Bertini, 2003; Suc & Popescu, 2005). For instance, rhinoceroses similar to *Stephanorhinus hundsheimensis* were the possible ecological substitutes for *Stephanorhinus etruscus.* The larger, mixed-feeder *Praemegaceros obscurus* replaced the browser *Eucladoceros*, and a more specialised form replaced the mixed-feeder *"Pseudodama" nesti.* It is worth noting that Breda & Marchetti (2007) doubtfully reported ?*Eucladoceros ex gr. ctenoides-dicranios* and ?*Megaloceros obscurus* from the main brown coal level (subunit 5) of the biogenetic unit of Leffe Formation (Bergamo, Northern Italy), but the actual co-occurrence of these large deer needs to be fully substantiated. Among carnivores, *Megantereon whitei*, a saber-tooth cat of African origin, first appeared.

The faunal renewal between the Farneta and Pirro FU (Table 2) is marked by the appearance of some arriving African taxa, such as the large *Hippopotamus antiquus* (Magri *et al.*, 2009), and (doubtfully) the cercopithecid *Theropithecus*, a mixed-feeding genus whose extant species inhabits the high grasslands of Ethiopia and Eritrea (Rook *et al.*, 2004, but see Patel *et al.*, 2007). This evidence of African immigration to southernmost Europe stresses the importance of "out of Africa" migratory waves, which occurred approximately around 1.6/1.3 Ma (Martinez-Navarro, 2004). Other immigrants had an Asian/European origin, as the ovibovine *Megalovis* and the rather stout bovine *Bison (Eobison) degiulii,* the latter replacing the slender leptobovines. Among perissodactyls, the middle-sized, slender limbed *Equus altidens* and the larger *Equus suessenbornensis* were certainly present, whereas *Equus stehlini* is no longer recorded (see Alberdi & Palombo, in press for a discussion). Among carnivores the middle-sized bone crusher *Canis mosbachensis* first appeared and *Lycaon (Xenocyon) lycaonoides* substituted the less advanced *L. falconeri.* The dispersal of

Homo in the Italian peninsula is testified by the finding of lithic implements in the karstic network of Pirro Nord, the local eponym of the Pirro FU (ARZARELLO *et al.,* 2007). All in all, forest-dwelling taxa dwindled, whereas species inhabiting prairies, savanna or steppes increased in percentage. The prevalence of dry and open environments at the time of the Pirro FU (and Colle Curti FU as well) is confirmed by the great structural compatibility of these faunas with those of present day savanna/bushland habitats (PALOMBO, 2007b). Nevertheless, forest areas were still rather abundant, and woodlands spread in the more temperate and humid climatic phases, as evidenced, for instance, by the presence of the browser moose *Cervalces carnutorum* in the subunit 7 of Leffe Formation (Bergamo, Northern Italy) (BREDA & MARCHETTI, 2005, 2007), which deposited shortly before the Jaramillo Subchron (MUTTONI *et al.*, 2007).

The occurrence at Pietrafitta (Umbria, central Italy) of a vole close to *Microtus (Allophaiomys)* ex gr. *M. ruffoi, and of Microtus (Allophaiomys) chalinei* and *Mimomys pusillus* in a large mammal fauna whose taxonomical composition and structure is consistent with that of the the Farneta FU (GENTILI *et al.*, 1996; BARISONE *et al.,* 2006; PALOMBO & GIOVINAZZO, 2006), as well the presence at Pirro Nord of a more evolved *Microtus (Allophaiomys)* ex gr. *M. ruffoi*, provide a correlation of the Farneta and Pirro FU with the earliest Biharian (Early Biharian I, MASINI & SALA, 2007). Accordingly, and taking into account magnetostratigraphical dating of Tuscan LFA's assigned to Olivola plus the Tasso FU, the Farneta and Pirro FU's developed during the pre-Jaramillo Early Pleistocene, but the actual chronological extent of each FU is based only on biochronological estimates.

3.4.2 Colle Curti FU and the beginning of the Mid Pleistocene revolution (MPR)

The transition from the Early to Middle Pleistocene, Mid-Pleistocene revolution (MPR) (from about 1.2 to 0.6 Ma) marks a fundamental change in the Earth's climate system (MASLIN and RIDGWELL, 2005) and represents a major episode in mammalian fauna reorganisation over the course of the Cenozoic. Orbital obliquity at 41-ka cycles was superseded progressively by a 100-125-ka rhythm, sustained by four-five precessional cycles, and accompanied by increased amplitude climatic oscillations (Table 2). Glacial phenomena intensified, temperature and moisture dropped notably, vegetational "exotic" essences, quite common in earlier floras, progressively disappeared and sustained climatic changes prevented these floral elements from becoming re-established (BERTINI, 2003). These changes spurred a shift in environments and constrained the geographical diffusion of a number of taxa, allowing dispersal waves that drove the reorganisation of large mammal communities. Community rebuilding came to an end during the beginning of the Middle Pleistocene with the disappearance of the last surviving Villafranchian species, such as *Pachycrocuta brevirostris and Panthera gombaszoegensis* (Table 3). Thus, at the time of MPR, fauna was characterised by the presence of long surviving Villafranchian taxa and by a progressive increase in taxa, which also persisted into the Middle Pleistocene. Such a framework of "mixed faunal elements" was regarded by authors either as a "transitional fauna"

(BONIFAY, 1978; AZZAROLI *et al.*, 1988) or a distinct biochron (e.g. Protogalerian sensu Caloi & Palombo, 1995, Epivillafranchian sensu Kahlke 2007 and previous papers; 'latest Villafranchian' sensu Koufos, 2001 or 'Final Villafranchian' SPASSOV, 2003). On the other hand, if Middle Pleistocene faunas are clearly to be considered as 'modern' when compared to those from the Villafranchian (PALOMBO, 2004b), which criteria should be used to define the 'theoretical' boundary between the Villafranchian and the following Galerian LMA? According to GLIOZZI *et al.* (1997) (Table 1), the beginning of the Galerian LMA would be conventionally marked by the appearance, among others, of *Praemegaceros verticornis*, which is first recorded in Italy at the Colle Curti LFA (Colle Curti FU, late Early Pleistocene, Jaramillo Subchron, COLTORTI *et al.*, 1998). This giant deer has been recently found in the Spanish Fuente Nueva 3 and the Barranco Leon LFA, dated at about 1.3 Ma (AGUSTÍ & MADURELL, 2003), which retain several Villafranchian taxa, as does the Colle Curti LFA. Moreover, the Pirro Nord (latest Villafranchian) and the Colle Curti LFA's exhibit a relatively high coefficient of similarity (PALOMBO & VALLI, 2005). Consequently, the Colle Curti LFA still looks closer to the latest Villafranchian LFA's than to the ensuing typical Galerian ones, despite the LISDk of *Praemegaceros verticornis*, *Cervalces latifrons* (BREDA & MARCHETTI, 2005)*,* and possibly of subgenus *Bison,* the significant reduction in biodiversity shown by carnivores, as well as the innovative characteristics of the arvicolids (SALA & MASINI, 2007).

All in all, the the Pirro and Colle Curti FU's correspond to a time slice during which the Villafranchian were gradually but not completely displaced by some typical Galerian large mammals foreshadowing the coming of a new age. This evidence encourages a redefinition of the Galerian LMA (cf. PALOMBO, 2004a and references therein, KAHLKE, 2007).

3.5. The MPR accomplishment and the onset of typical Galerian mammalian faunas

As above mentioned, the faunal renewal leading to the typical Galerian faunas finds its origin in two distinct trends: 1) the progressive reduction in richness characterising late Early Pleistocene faunas (from the Farneta to the Colle Curti FU's), 2) the subsequent dispersal and the progressive spread in Italy of taxa from Eastern and Central Europe, that triggered a rapid increase in diversity at the beginning of the Middle Pleistocene (Slivia FU) (PALOMBO 2007b and references therein). It is noteworthy that this faunal change involved both carnivore and herbivore guilds at various times. The most important change in the former had already taken place prior to the Jaramillo Subchron, at the Pirro–Colle Curti FU's transition, with the disappearance of some large taxa, either flesh-eaters or bone-breakers, such as large canids and felids (Table 3) (PALOMBO *et al.*, 2008 and references therein). This is the starting point for a reversal in the proportion of carnivores versus herbivores: indeed, across the Early to Middle Pleistocene (Slivia FU), the faunal renewal was strongly biased in favour of large herbivores, while the carnivore guild changed at a slower pace. Taxa dispersed from Eastern and Central Europe reached the Italian peninsula in succession, thus leading an important and relatively

rapid increase in diversity at the beginning of the Middle Pleistocene. These changing faunas represent a major large mammal community reorganisation throughout the Quaternary. This dispersion phase was probably triggered by notable climatic changes that correspond to the onset of the pronounced glacial–interglacial fluctuations as observed in the marine isotope record during the late Early Pleistocene (MIS 25 to 22-20), while the progressive increase in diversity is seen as a consequence of the ensuing onset of wetter climatic conditions (see PALOMBO & GIOVINAZZO, 2006 and references therein). Instead of replacing any one species, these taxa enriched the herbivore guild, as well as the large mammal community as a whole (Palombo, 2007b and references therein). Even if, on a larger temporal scale, the progressive modification in the structure of large mammal faunas of the Italian peninsula began before the Jaramillo Subchron, it was shortly before the Early to Middle Pleistocene boundary that the major renewal and important ecological reorganisation of faunal complexes took place (PALOMBO, 2007b).

Throughout the course of time (Table 3), the local appearances of several pachyderms (*Elephas (Palaeoloxodon) antiquus, Mammuthus trogontherii, Stephanorhinus kirchbergensis, Stephanorhinus hemitoechus*), large (*Megaloceros savini, Praemegaceros solilhacus*), and medium-sized deer (*Capreolus capreolus suessenbornensis, Cervus elaphus acoronatus* and possibly *Dama clactoniana*), as well as large (*Hemibos galerianus, Bos primigenius*) and middle-sized bovids (*Ovis ammon antiqua, Hemitragus bonali*), together with caballine horses (*Equus mosbachensis*), all mainly mixed feeders or grazers, inhabiting open landscapes, bushlands or wooded grasslands, brought about a major change in the herbivore guilds (PALOMBO, 2007b). Among carnivores, *Crocuta crocuta* first appeared (Ponte Galeria 2 LFA, PG2 sequence, about 750-650ka, MILLI & PALOMBO, 2005 and references there in), whereas some other large carnivores, active hunters that were both flesh-eaters and scavengers [such as *Ursus deningeri, Panthera fossilis*, Isernia LFA, about 600 ka (COLTORTI et al., 2005); a hyaena, Hyaena prisca, whose taxonomical identification is still matter of debate at the Ponte Galeria 3 LFA (see CALOI & PALOMBO, 1980; PALOMBO et al., 2008; TURNER et al., 2008), PG3 about 650-550 ka (MILLI & PALOMBO, 2005); *Panthera pardus*, Valdemino Cave LFA, Isernia FU (SALA, 1992) and Isernia LFA (SALA, 2006)], had their lowest stratigraphical occurrence even later. These species, together with *S. hundsheimensis, Equus altidens, E. suessenbornensis, P. verticornis* and *B. shoetensacki* are eponymous of the "typical" Galerian faunas.

Most authors recognise in the "middle" Galerian (sensu Gliozzi et al., 1997) two FU's, Slivia and Isernia which are clearly differentiated by the small mammals: *Mymomys savini* (Slivia LFA) and *Arvicola mosbachensis* (Isernia LFA). The small mammal association found at the archaeological site Isernia La Pineta (Molise), represents the oldest Toringian fauna recorded in Italy to date (SALA & MASINI, 2007) and represents the main renewal of small mammals throughout the Galerian LMA.

PETRONIO and SARDELLA (1999) proposed the introduction of the Ponte Galeria FU (Table 1), by these authors regarded as intermediate in taxonomical composition, and in age as well, between the Slivia and Isernia FU's. This, because of the persistence of *Pachycrocuta brevirostris* and *Panthera gombaszoegensis* in the Slivia FU, the exclusive occurrence of *Hemibos galerianus* in the "Ponte Galeria FU" and the appearance of *Bos primigenius* in the Isernia FU. Nevertheless, Slivia and Ponte Galeria 2 LFA's would be assumed to be part of the same FU due to the uncertain identification of some herbivores from Slivia LFA, and the assumption that carnivores absent from the Ponte Galeria CU have in fact been found in the Slivia LFA. Unfortunately, there are no stratigraphical constraints for the age of the Slivia FU, even if it can be correlated with the Late Biharian, which roughly extends from 0.95 to 0,6 Ma, due to the occurrence of *M. savini* associated with that of *Microtus (Stenocranius)* and *Microtus (Terricola)*. Conversely, in the Roman basin, the integrated mammal biostratigraphy and sequence stratigraphy approach represents a valid tool to identify and to correlate physical and biological events. The biochronological and sequence-stratigraphical scheme proposed for the Ponte Galeria area, highlights that the sequence stratigraphical framework can constrain the possible chronological interval in which a bioevent, even if local, occurred (see MILLI & PALOMBO, 2005).

The transition from the middle to late Galerian (Fontana Ranuccio FU) possibly occurred around 550–500 ka, due to the absolute age available for the LFA's ascribed to Isernia FU (Notarchirico and Isernia LFA's, estimated age about 600 ka by LEFÉVRE & RAYNAL, 1999; Lefévre et al., 1999; and COLTORTI et al., 2005, respectively), and the Fontana Ranuccio FU (Fontana Ranuccio LFA, estimated age about 458 ka, BIDDITTU et al., 1979).

During the late middle Galerian (Fontana Ranuccio FU), "Villafranchian" taxa were not yet recorded and the number of very large herbivores diminished (Table 3). The occurrence of "Galerian" equids and megacerines is doubtful and the specialised and slightly larger *H. antiquus was* replaced by *Hippopotamus amphibius* and, among carnivores, *Ursus arctos* appeared as well as *Felis silvestris* (Table 3).

In the second half of the Middle Pleistocene, increasingly different habitats supported increasingly varied faunas (cf. TRIANTIS et al., 2003), with new dynamic interspecific relationships. In fact, with the end of the Galerian (Fontana Ranuccio FU) and the transition to the following Aurelian LMA, the most flexible species became the dominant group, the percentage of browsers increased and fauna progressively acquired modern characteristics (PALOMBO 2007b and references therein).

3.6 The Aurelian LMA and the Middle to late Pleistocene boundary

GLIOZZI et al. (1997) proposed the Aurelian as a new LMA, differing from the Galerian LMA because of the appearance of taxa that constitute the core of the modern mammalian fauna, whereas some "Galerian"species (such as horses, megacerine deer, medium-sized, bovid *Ovis ammon antiqua and Hemitragus bonali*, and large bovide, *Bison shoetensacki)* were no longer pre-

sent. According to GLIOZZI et al. (1997), three distinct, main faunal complexes could be detected: early, middle and late Aurelian, characterised by an increase in the percentage of modern taxa. The early and middle Aurelian were subdivided on the basis of faunal differences between two already created FU's, Torre in Pietra and Vitinia (CALOI and PALOMBO 1990, 1996, but see below), while for the late Aurelian (MIS 5-2) no characteristic FU's have correctly been designated due to the monotonous taxonomical composition of the last interglacial faunas, as well the only sporadic occurrence of the so called "cold taxa" during the last Glacial (but see PETRONIO et al, 2007).

3.6.1 The Aurelian LMA and the question of Vitinia FU

The Torre in Pietra and Vitinia FU's have been defined on the basis of palaentological and stratigraphical evidence collected in the Roman Basin (CALOI et al., 1998; but cf. PALOMBO et al., 2004 and references therein). Along the Latium coast, rich LFA's (Torre in Pietra, La Polledrara di Cecanibbio, Collina Barbattini, Castel di Guido, Malagrotta) have been recovered either from fossiliferous deposits of the Aurelia Formation (CONATO et al., 1980) or the PG6 sequence, both correlated with MIS 9 (MILLI & PALOMBO, 2005). In these LFA's, assigned to the Torre in Pietra FU the LISDk of Canis lupus, Ursus spelaeus and Megaloceros giganteus is reported. In the same area, LFA's uncovered in fossiliferous levels of the Vitinia Formation (CONATO et al., 1980) or PG7 sequence (MILLI, 1997), correlated with MIS 7 (e.g. Torre in Pietra upper levels, Vitinia level e, Cerveteri) (PALOMBO et al., 2003 and references therein) were previously ascribed to the Vitinia FU's (CALOI & PALOMBO, 1995; CALOI et al., 1998) essentially because of the abundance of a primitive fallow deer, Dama dama tiberina (locally associated with the pre-existing larger Dama dama clactoniana), as well the appearance, among others of Cervus elaphus with features similar to those of modern red deer and of Equus hydruntinus. Nevertheless, the structure and the taxonomical composition of the Torre in Pietra and Vitinia faunal complexes are similar (PALOMBO & MUSSI, 2001; PALOMBO 2004), thus the division into two FU's seems to be based on weak palaentological data, moreover new stratigraphical evidences call for a revision of these biochrons. In the 1990's, two LFA's, Sedia del Diavolo and Monte delle Gioie (today, no longer exposed due to of the intense urbanization of Rome after World War II), were assigned to the Vitinia FU due to the abundance of Dama dama tiberina remains in the alluvial deposits overlaying the "Tufo lionato" (a lithified pyroclastic flow deposit from Albani Volcanic Complex, dated 355 ka by KARNER et al., 2001) where also Equus hydruntinus was found (CALOI & PALOMBO, 1995). CALOI et al., (1998) correlated these bone-bearing deposits with the Vitinia Formation (MIS 7), but recently the overlain ash flow has been dated at 285 ± 1 ka (MARRA & ROSA, 1995; KARNER et al., 2001). Following this new chronological data, the deposition of the fluvio-lacustrine sediments overlaying the "Tufo lionato" at Sedia del Diavolo, occurred approximately during the time span between 355 and 285 ka (PALOMBO et al., 2004).

Accordingly, the LISDk Dama dama tiberina in Italy is documented in deposits correlated with the MIS 9, thus the Vitinia FU cannot be considered a valid biochron. The LFA's previously ascribed the Torre in Pietra and the Vitinia FU's have to be included in a single FU (named Torre in Pietra FU for priority reason) (Table 1).

Summarizing, several bioevents characterised the beginning of the Torre in Pietra FU, as well as the beginning of the Aurelian LMA (subdivided into early and late Aurelian) as here redefined: for instance Canis lupus first appeared as well as Ursus spelaeus that substituted U. deningeri, Megaloceros giganteus, Dama dama "tiberina, and Bubalus murrensis (PALOMBO, 2007 and unpublished data), the "steppe horse E. hydruntinus dispersed along the Italian peninsula. Furthermore, some new medium-sized taxa appeared, when more severe, arid climatic oscillations favoured the spread of "mountain" bovids (Capra ibex and Rupicapra) towards the southernmost regions of the Italian peninsula, whereas Galerian megacerine deer and horses, Ovis ammon antiqua and Bison shoetensacki are no longer recorded (Table 3).

All in all, with the end of the Galerian (Fontana Ranuccio FU) and the transition to the Aurelian (Torre in Pietra FU), the most flexible species became the dominant group, the percentage of browsers increased and fauna progressively acquired modern characteristics. This is consistent with a moderate woodland expansion under increasingly mild climatic conditions characterising the interglacial phases, as well as the increase in north to south and east to west climatic gradients leading to the fragmentation of Italian habitats.

The structure of Aurelian mammalian faunas was fully attained long before the beginning of the beginning Late Pleistocene, thereby the transition from Galerian to Aurelian LMA predated the Middle to Late Pleistocene boundary.

3.6.2 The Late Pleistocene

The Last Interglacial LFA's did not substantially differ from those recorded during the late Middle Pleistocene. The rare species Bubalus murrensis is no longer present, while modern fallow and red deer substitute the late Middle Pleistocene subspecies, but the core of the early Aurelian faunas keeps roughly unchanged. Although the Last Glacial phase caused a remarkable shift in the vegetational cover and in the distribution of mammals in Europe, minor changes characterised the transition from the Last Interglacial to the Last Glacial faunal complexes on the Italian peninsula (PALOMBO, 2007b). During the last Glacial, the faunal biodiversity increased with the arrival of some "cold" species, such as the typical, Mammuthus primigenius, the woolly rhinoceros Coelodonda antiquitatis, the elk Alces alces, inhabiting a "mammoth steppe"-like environment extending throughout the Eastern Po Valley (GALLINI & SALA, 2001). Mammoth and woolly rhinoceros, as well the wolverine, Gulo gulo, reached the Tyrrhenian coast (Latium) and were widespread in the south-eastern part of the Italian peninsula, where Alopex lagopus is also recorded, while Rangifer tarandus only reached the westernmost geographical boundary of the Italian coast (CALOI & PALOMBO, 1995; SALA, 2005). The spread of "cold" species across the Italian peninsula was profoundly conditioned by microclimate and physiography, and the taxonomical compo-

sition and structure of LFA's could vary greatly, depending on the geographical position of fossiliferous sites. That, coupled with the high percentage of extant species, prevent any FU to be fairly defined. Moreover, the faunal assemblages were progressively depleted of some long-surviving Galerian species. Pachyderms were most affected by climatic deterioration. *Hippopotamus* survived only until the end of the MIS 5a, whereas *Elephas antiquus* occurred also during MIS 4 and *Stephanorhinus* was still present during MIS 3, while *Panthera spelaea* survived till the beginning of the Holocene (Boschian *et al.,* 1995).

All in all, the mammal faunas on the Italian mainland maintained "temperate-cool" characteristics even during the cold-arid peaks of the Last Glacial. Broadleaved wooded release "refugial" areas always existed on the Tyrrhenian side of the peninsula, while the climate on the Adriatic side was probably drier. Therefore, some "warm" species remained on the Italian peninsula longer than elsewhere, and turnovers in successive communities were less dramatic than in northern Europe. With the deglaciation phase at the beginning of the Holocene, dramatic moisture and vegetation change led to marked changes in mammalian faunas, particularly in their abundance, leading to the megafauna extinction.

4. CONCLUSION

Several evidences show that, at least as far as the Italian peninsula is concerned, global climatic changes are a contributing factor, especially in the first appearances of large mammals. This permitted the dispersal of new taxa, because mammals frequently reacted to the Plio-Pleistocene climate changes, expanding their distribution area or migrating rather than by evolving and producing new species.

Climate change, via migrations and dispersal events, caused diversity bursts but altered palaeocommunity equilibria, leading to new intra- and inter-guild dynamics. We can also hypothesize that cause-and-effect relationships between climatic oscillations and faunal changes may be the cumulative result of the responses of individual species and that climatic changes could have caused the removal of keystone species. Accordingly, migratory responses to climate change and physical-environmental disturbances, together with biotical interactions mainly contributed to faunal evolution in successive phases by discrete bioevents, maybe diachronous even in a restricted geographical area such as the Western Europe. This fact prevents any detailed biochronological framework from having wide geographical significance and predisposes it to change in the light of new findings. This is, e.g., the case of weakly defined FU's such as the Italian "Saint Vallier" (Gliozzi *et al.,* 1997) and the Vitinia (Caloi & Palombo, 1990) FU's, which stratigraphical evidences forced its deletion. Moreover, increasing palaeontological and stratigraphical data sometimes leads us to better discriminate bioevents, highlighting the gradual renewal between successive biochrons, but blurring their clear identification as in the case of the Olivola and Tasso FU's. Thus, only higher rank biochronological units (Land Mammal Ages, LMAs) - whose separation is

based on palaeobiological events which have a wide territorial significance - could be useful for chronological correlations. Nonetheless, the transition between successive LMAs does not always correspond to the boundaries separating marine Series or Stages. For instance, the Villafranchian LMA approximately began with the Late Pliocene (Piacentian) and the transition from the early to the middle Villafranchian LMA happened around the Pliocene/Pleistocene (Piacentian/Gelasian) boundary, whereas the transition to the late Villafranchian took place during the latest Gelasian, and those from the Villafranchian to Galerian LMA and from the Galerian to Aurelian LMA respectively predated the beginning of the Middle and Late Pleistocene. Concerning the Villafranchian to Galerian LMA transition, from what has been previously reported on the biochronological patterns of large mammals, it possibly occurred close to MIS 25, where Cita & Castradori (1995, but see Cita *et al.,* 2006) previously proposed lowering the Early to Middle Pleistocene Boundary.

ACKNOWLEGEMENT

REFERENCES

Aguirre E. & Pasini G. (1985) - *The Pliocene-Pleistocene Boundary*. Episodes, **8** (2), pp. 116-120.

Agusti, J. & Madurell, J. (2003) - Los arvicolidos (Muroidea, Rodentia, Mammalia) del Pleistoceno inferior de Barranco Leon y Fuente Nueva 3 (Orce, Granada). Datos preliminares. In: Toro, I., Agusti, J. & Martinez-Navarro , B. (Eds): *El Pleistoceno inferior de Barranco Leon y Fuente Nueva 3, Orce (Granada)*. Junta de Andalusia. Consejeria de Cultura: 137-146, Sevilla

Alberdi M.T. & Palombo M.R. (in press) - *The Equidae of the Early Pleistocene site of Pirro (Southern Italy).* Palaeontographica

Alberdi M.T., Ortiz Jaureguiza, E. & Prado J.L. (1998) - *A quantitative review of European stenonoid horses.* Journal of Paleontology, **72**, pp. 371-387.

Ambrosetti P., Azzaroli A., Bonadonna F.P. & Follieri M. (1972) - *A scheme of Pleistocene chronology for the Tyrrhenian side of Central Italy.* Bollettino della. Società geologica italiana, **91**, pp. 169-184.

Arzarello M., Marcolini F., Pavia G., Pavia M., Petronio C., Petrucci M., Rook L. & Sardella R. (2007) - *First evidence of early Homo occupation in Europe: the site of Pirro Nord (southern Italy).* Naturwissenschaften, **94**, pp. 107112

Azzaroli A. (1977) - *The Villafranchian Stage in Italy and the Plio-Pleistocene Boundary.* Giornale di Geologia, **41**, pp. 61-79.

Azzaroli A. (1982) - *Remarques sur les subdivisions chronologiques du Villafranchien.* Actes Colloque "Le Villafranchien Mediterranéen", Lille 9-10 décembre 1982, **1**, pp. 7-14.

Azzaroli A. (1983) - *Quaternary mammals and the "End-Villafranchian" dispersal event - A turning point in the history of Eurasia.* Palaeogeography, Palaeoclimatology, Palaeoecology, **44**, pp. 117-139.

Azzaroli A. (1995) - *The 'Elephant-Equus' and the 'End-Villafranchian' events in Eurasia*. In: Vrba E. S., Denton G. H., Partridge T. C. & Burckle L. H. (Eds): Paleoclimate and Evolution with Emphasis on Human Origins. New Haven and London (Yale University Press, pp. 311–318.

Azzaroli A., De Giuli C., Ficcarelli G. & Torre D. (1988) - *Late Pliocene to Early Mid-Pleistocene mammals in Eurasia: Faunal succession and dispersal events.* Palaeogeography, Palaeoclimatology, Palaeoecology, **66**, pp. 77-100.

Barisone G., Argenti P. & Kotsakis T. (2006) - *Plio-Pleistocene evolution of the genus Castoro(Rodentia, Mammalia) in Europe:* C. fiber plicidens *of Pietrafitta (Perugia, Central Italy).* Geobios, **39**, pp. 757-770.

Bedetti C., Palombo M.R. & Sardella R. (2001) - *Large mammals and birds last occurrences in the Late Pleistocene of Italian peninsula.* In: Cavaretta G., Gioia P., Mussi M. & Palombo M.R. (Eds), The World of Elephant, CNR, Roma, pp. 701-703.

Benvenuti M., Dominici S. & Rook L. (1995) - *Inquadramento stratigrafico- deposizionale delle faune a mammiferi villafranchiane (unita faunistiche Triversa e Monopoli) del Valdarno Inferiore nella zona a sud dell'Arno (Toscana)*. Il Quaternario 8, 457–464.

Berggren W.A. & Van Couvering J.A. (1978). *Biochronology.* In Cohee G.V., Glaessner M.F. & Hedberg H.D. (Eds): *Contribution to the Geologic Time Scale*. American Association of Petroleum Geologists Bulletin, **50**, pp. 1487-1500.

Bertini A. (2003) - *Early to middle Pleistocene changes of the Italian flora and vegetation in the light of a chronostratigraphic framework*. Il Quaternario **16**(1bis), pp. 19-36.

Bertini A. & Roiron P. (1997) - *Evolution de la végétation et du climat pendant le Pliocène moyen en Italie centrale: apport de la palynologie et des macroflores à l'étude du bassin du Valdarno Supérieur, (coupe de Santa Barbara)*. Comptes Rendus de l'Académie des Sciences de Paris, Sér. 2a, **324**, pp. 763–771

Biddittu I., Cassoli P.F., Radicati Di Brozolo, F., Segre A.G., Segre Naldini, E. & Villa, I. (1979) - *Anagni, a K-Ar dated Lower and Middle Pleistocene Site, Central Italy: Preliminary report*. Quaternaria, **21**, pp. 53-71.

Bonifay M.-F. (1978) - *Faunes de transition du Pléistocène moyen de France.* Bulletin du Museum d'Anthropologie et Préhistoire de Monaco, **22**, pp. 5–15.

Boschian G. Mallegni F. & Tozzi C. (1995) - *The Epigravettian and Mesolithic site of Fredian Shelter (in Tuscany).* Quaternaria Nova, **5**, pp. 45-80.

Bowen D.Q. & Gibbard P. L. (2007) - *Quaternary is here to stay*. Journal of Quaternary Science. **22** (1), pp. 3-8

Breda M. & Marchetti M. (2005) - *Systematical and biochronological review ofPlio-Pleistocene Alceini (Cervidae; Mammalia) from Eurasia.* Quaternary Science Rewies, **24**, pp.775-805.

Breda M. & Marchetti M. (2007) - *Pleistocene mammal faunas from the Leffe Basin (Bergamo, Northern Italy): revision and new data*. Courier Forsch. Inst. Senckenberg **259,** pp. 61-77.

Caloi & Palombo, 1995,

Caloi L. & Palombo M.R. (1990) - *Osservazioni sugli equidi italiani del Pleistocene medio inferiore.* Geologica Romana, **26** (1987), pp. 187-221,

Caloi L., Palombo M.R. (1995) - *Le mammalofaune del Pleistocene inferiore nell'Italia centrale.* Studi Geologici Camerti, vol. spec. **1994 (B)**, pp. 487-501

Caloi L. & Palombo M.R. (1996) - *Latest Early Pleistocene mammal faunas of Italy, biochronological problems.* Il Quaternario, **8** (2), pp. 391-402

Caloi L., Palombo M.R. & ZARLENGA, F. (1998) - *Late Middle Pleistocene mammals faunas of Latium; stratigraphy and environmen.* Quaternary International, **47/48,** pp. 77-86.

Cita M. B. & Castradori D. (1995) - *Workshop on marine sections from the Gulf of Taranto (Southern Italy) usable as potential stratotypes for the GSSP of the Lower, Middle and Upper Pleistocene.* Il Quaternario, **7** (2), pp. 677–692.

Cita B.M., Capraro L., Ciaranfi N., Di Stefano E., Marino M., Rio D., Sprovieri R. & Vai G.B. (2006) - *Calabrian and Ionian: A proposal for the definition of Mediterranean stages for the Lower and Middle Pleistocene.* Episodes, **29**(2), pp. 107-113.

Coltorti M., Albianelli A., Bertini A., Ficcarelli G., Laurenzi M.A., Napoleone G. & Torre, D. (1998) - *The Colle Curti mammal site in the Colfiorito area (Umbria-Marchean Apennine, Italy): geomorphology, stratigraphy, paleomagnetism and palynology.* Quaternary International **47/48**, pp. 107-116.

Coltorti M., Feraud G., Marzoli A., Peretto S., Ton-That C., Voinchet T.P., Bahain J.-J., Minelli A. & Thun Hohenstein U. (2005) - *New 40Ar/39Ar, stratigraphic and palaeoclimatic data on the Isernia La Pineta Lower Palaeolithic site, Molise, Italy.* Quaternary International, **131**, pp. 11–22.

Conato V., Esu D., Malatesta A. & Zarlenga F. (1980) - *New data on the Pleistocene of Rome.* Quaternaria, **22**, pp. 131–176.

De Giuli C. & Masini F. (1987) - *Late Villafranchian faunas in Italy: the Casa Frata Local Fauna (Upper valdarno, Tuscany).* Palaeontographica Italica **74**: 1–9.

De Giuli C., Ficcarelli G., Mazza P. & Torre D. (1983) - *Confronto tra successioni marine e continentali del Pliocene e Pleistocene inferiore in Italia e nell'area mediterranea.* Bollettino della Società Paleontologica italiana, **22**, pp. 323-328.

Ding Z., Rutter N.W., & Liu T. (1997) - *The onset of extensive loess deposition around the G/M boundary in China and its palaeoclimatic implications.* Quaternary International, **40**, pp. 53-60.

Gallini V. & Sala B. (2001) – Settepolesini di Bondeno (Ferrara -Eastern Po Valley): the first example of

Mammoth steppe in Italy. In: Cavarretta G., Gioia P., Mussi M., & Palombo M.R. (Eds), The World of Elephants, CNR, Rome, pp. 272-275.

GARRIDO G. (2008) - El registro de *Vulpes alopecoides* (Forsith-Major, 1877); *Canis etruscus* Forsith-Major, 1877 y *Canis* cf. *falconeri* Forsith-Major, 1877(Canidae, Carnivora, Mamalia) en Fonelas P-1 (Cuenca de Guadix, Granada).In ARRIBAS HERRERA A. (Ed.) Vertebrados del Plioceno superior terminal en el suroeste de Europa: Fonelas P-1 y el *Proyecto Fonelas.* Publicaciones del Instituto Geologico de Espana, Cuadernos del Museo Geominero, 10, 159-186.

GENTILI S, ABBAZZI L, MASINI F, AMBROSETTI P, ARGENTI P. & TORRE D. (1996) - *Voles from the Early Pleistocene of Pietrafitta (central Italy, Perugia).* Acta Zoologica Cracoviensia, **39**(1), pp. 185–199.

GENTILI S. & MASINI F. (2005) - *An outline of Italian Leptobos and a first sight on Leptobos aff. vallisarni from Pietrafitta (early Pleistocene, Perugia).* Quaternarie, Hors Series **2**, 81–89.

GHINASSI M., MAGI M., SAGRI M. & SINGER B.S. (2004) - *Arid climate 2.5 Ma in the plio–pleistocene Valdarno Basin (Northern Apennines, Italy).* Palaeogeography, Palaeoclimatology, Palaeoecology **207**, pp. 37–57.

GIBBARD P. & HEAD M.J. (2009) - *The definition of the Quaternary System/Era and the Pleistocene Series/Epoch.* Quaternarie **20** (2), 125-133.

GLIOZZI E., ABBAZI L., AMBROSETTI P., 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, Ostracods from the Middle Pliocene to the Late Pleistocene in Italy. The state of the art.* Rivista Italiana di Paleontologia i Stratigrafia, **103** (3), pp. 369-388.

GRICHUK V.P. (1997) - *Late Cenozoic change in flora in extra-tropical Eurasia in the light of palaeomagnetic stratigraphy.* In: VAN COUVERING E. (Ed.), The Pleistocene boundary and the beginning of the Quaternary. Cambridge University Press, pp. 104-113.

GUERIN C. (1982) - *Première biozonation du Pléistocène européen: principal résultat biostratigraphique de l'étude des Rhinocerotidae (Mammalia, Perissodactyla) du Miocène terminal au Pléistocène supérieur d'Europe occidentale.* Geobios, **15**, pp. 593-598.

GUERIN C. (1990) - *Biozones or Mammal Units? Methods and Limits in Biochronology.* In: Lindsay, E.H., Fahlbusch, V. & Mein, P. (Eds): European Neogene Mammal Chronology, pp. 119-130; Plenum Press, New York.

HEMMER H., KAHLKE R.D., KELLER T. (2003) - *Panthera onca gombaszogensis (Kretzoi, 1938) from the early middle Pleistocene Mosbach sands (Wiesbaden, Hessen, Germany) a contribution to the knowledge of the variability and history of the dispersal of the jaguar.* Neues Jahrbruch für Geologie und Paläontologie Abhandlungen, **229**, pp. 31–60.

KAHLKE R.-D. (2007) - *Late Early Pleistocene European large mammals and the concept of an Epivillafranchian biochron.* Courier-Forschungsinstitut Senckenberg, **259**, pp. 265-278.

KARNER D.B., MARRA F. & RENNE P.R. (2001) - *The history of the Monti Sabatini and alban Hills volcanoes: groundwork for assessing volcanic-tectonic hazards for Rome.* Journal of Volcanology and Geothermal Research **107**, pp. 185–219.

KOUFOS G.D. (2001) - *The villafranchian mammalian fauna and biochronology of Greece*. Bollettino della Societa` Paleontologica Italiana **40**, pp. 217–223.

Lacombat *et al*., 2008

LACOMBAT F., ABBAZZI L., FERRETTI M.P., MARTÍNEZ-NAVARRO B., MOUL P.-E., PALOMBO M.R., ROOK L., TURNER A. & VALLI A.M.F. (2008) - *New data on the Early Villafranchian fauna from Vialette (Haute-Loire, France). Collection of the Crozatier Museum (Le Puy-en-Velay, Haute-Loire, France).* Quaternary International. **179** (1), pp. 64-71

LEFÈVRE, D. & RAYNAL, J.P. (1999) - Etudes géologique à Notarchirico et dans le bassin de Venosa: premier bilan et perspectives. In: Piperno, M. (Ed.): *Notarchirico. Un sito del Pleistocene medio iniziale nel bacino di Venosa*: 253- 258. Edizioni Osanna, Italia.

LEFÈVRE, D., RAYNAL, J.P. & VERNET, G. (1999) - Enregistrements pléistocènes dans le bassin de Venosa. In M. Piperno (Ed.): *Notarchirico. Un sito del Pleistocen medioiniziale nel bacino di Venosa*": 139-174; Edizioni Osanna, Italia.

LINDSAY E. (2003) - *Chronostratigraphy, Biochronology, Datum Events, Land Mammal Ages, Stage of Evolution, and Appearance Event Ordination*. Bulletin of the American Museum of Natural History: No. **279**, pp. 212–230.

LINDSAY E.H., OPDYKE N.D. & JOHNSON N.M. (1980) - *Pliocene dispersal of the horse Equus and Late Cenozoic mammalian dispersal events.* Nature, **287**, pp. 135–138.

LINDSAY E.H., OPDYKE N.D. & FEIJFAR O. (1995) - *Correlations of selected late Cenozoic mammal faunas with the magnetic polarity time scale.* Terra nostra, **2/95**, pp. 164.

LINDSAY H. & TEDFORD R.H. (1990) - *Development and application of Land Mammal Ages in North America and Europa, and comparison.* In: LINDSAY H., FAHLBUSCH W. & MEIN P. (Eds): European Neogene mammal Chronology. Plenum Press, New York, pp. 601-624.

MAGRI D., DI RITA F. & PALOMBO M.R. (2009) - *An Early Pleistocene interglacial record from an intermontane basin of central Italy (Scoppito, L'Aquila).* Quaternary International, doi: 10.1016/j.quaint. 2009.04.005.

MARRA F. & ROSA C. (1995) - *Stratigrafia e assetto geologico dell'area romana.* Memorie Descrittive della Carta Geologica d'Italia, **50**, pp. 49-118.

MASINI F. & SALA B. (2007) - *Large- and small-mammal distribution patterns and chronostratigraphic boundaries from the Late Pliocene to the Middle Pleistocene of the Italian peninsula.* Quaternary International, **160** (1), pp. 43-56.

MASLIN M. A. & RIDGWELL A. J. (2005) - *Mid-Pleistocene revolution and the 'eccentricity myth*. In: HEAD M.

J. & GIBBARD P.L. (Eds): Early–Middle Pleistocene Transition: The Land- Ocean Evidence. Geological Society, London, Special Publications, **247**: 19–34

MILLI S. & PALOMBO M.R. (2005) - *The high-resolution sequence stratigraphy and the mammal fossil record: a test in the Middle–Upper Pleistocene deposits 251 of the Roman Basin (Latium, Italy).* Quaternary International, **126 –128**, pp. 251-270.

MILLI S. (1997) - *Depositional setting and high-frequency sequence stratigraphy of the Middle-Upper Pleistocene to Holocene deposits of the Roman Basin.* Geologica Romana, **33**, pp. 99-136.

MUTTONI G., RAVAZZI C., BREDA M., PINI R., LAJ C., KISSEL C., MAZAUD A. & GARZANTI E. (2007) -*Magneto-stratigraphic dating of an intensification of glacial activity in the southern Italian Alps during Marine Isotope Stage 22.* Quaternary Research, **67**, pp. 161–173.

NAPOLEONE G., ALBIANELLI A., AZZAROLI A., BERTINI A., MAGI M. & MAZZINI M. (2003) - *Calibration of the Upper Valdarno Basin to the plio–pleistocene for correlating the Apennine continental sequences.* Il Quaternario, **16**, pp. 131–166.

OLIVE F. (2006) - *Evolution des grands Carnivores au Plio Pléistocène en Afrique et en Europe occidentale.* L'Anthropologie, **110** (5), pp. 850–869.

PALOMBO M.R. (2004a) - *Biochronology of the Plio-Pleistocene mammalian faunas of Italian peninsula: knowledge, problems and perspectives.* Il Quaternario, **17** (2/2), pp. 565-58.

PALOMBO M.R. (2004b) - *Guild of large Mammals from the Pliocene to the Late Pleistocene in the Italian peninsula.* In Baquedano, E. & Rubio, S. (Eds). *Homenaje a Emiliano Aguirre.* Zona Archeologica 4 (2 Paleontologia), Museo Arqueológico Regional, Madrid: pp. 372 391.

PALOMBO M.R (2007a) - *Which boundary for the Quaternary period and Pleistocene epoch? The contribution to the debate given by turnover patterns in large mammalian complexes from North-Western Mediterranean region.* Quaternaire, **18**(1), pp. 35-53.

PALOMBO M.R. (2007b) - *Large Mammal Guilds on the Italian Peninsula from the Pliocene to the Late Pleistocene: new methodological approaches.* Courier Forschungsinstitut Senckenberg, **259,** pp. 13-46.

PALOMBO M.R., AZANZA B. & ALBERDI M.T. (2003) - *Italian mammal biochronology from Latest Miocene to Middle Pleistocene: a multivariate approach.* Geologica Romana, **36** (2000-2002), pp. 335-368.

PALOMBO M.R & M.P. FERRETTI (2005) - Elephant fossil record from Italy: knowledge, problems, and perspectives. *Quaternary International*, **126 –128**, pp. 107-136.

PALOMBO M.R & GIOVINAZZO C. (2006) - *What do cenograms tell us about mammalian palaeoecology? The example of Plio-Pleistocene Italian faunas*. Courier Forschungsinstitut Senckenberg, **256,** pp. 215-235.

PALOMBO M.R., MILLI S & ROSA C. (2004) - *Remarks on the late Middle Pleistocene biochronology of the mammalian faunal complexes of the Campagna Romana.* Geologica Romana, **37** (2003), pp. 135-14.

PALOMBO M.R. & MUSSI M. (2001) - *Human presence and faunal evolution in the Middle Pleistocene of Italy.* Bollettino della Società Paleontologica Italiana, **40** (2), pp. 257-267

PALOMBO M.R., SARDELLA R. (2007) - *Biochronology versus Biostratigraphy: a true dilemma or a false trouble? The example of the Plio-Pleistocene large mammalian faunas from the Italian peninsula.* Quaternary International*, **160,** pp. 30-42.

PALOMBO M.R., SARDELLA R. & NOVELLI M. (2008) - *Carnivora dispersal in Western Mediterranean during the Quaternary.* Quaternary Internationa, **179** (1), pp. 176-189.

PALOMBO M.R. & VALLI A.F.M. (2005) - *Highlighting the Early–Middle Pleistocene transition in Italian and French large mammal faunas: similarities and faunal renewals.* In HEAD, M.J.& GIBBARD, P.L. (Eds): Early–Middle PleistoceneTransitions: The Land–Ocean Evidence. Geological Society, London, Special Publications, **247**, pp. 263-276.

PARTRIDGE T. C. (1997) - *Reassessment of the position of the Plio- Pleistocene boundary: is there a case for lowering it to the Gauss-Matuyama palaeomagnetic reversal?* Quaternary International, **40**, pp. 5–10.

PATEL B.A., GILBERT C.G. & ERICSON K.E. (2007) - *Cercopithecoid cervical vertebral morphology and implications for the presence of Theropithecus in early Pleistocene Europe.* Journal of Human Evolution, **52** (2), pp. 113-129.

PETRONIO C. & SARDELLA R. (1999) - *Biochronology of he Pleistocene mammal fauna from Ponte Galeria (Rome) and remarks on the Middle Galerian faunas.* Rivista Italiana di Paleontologia e Stratigrafia, **105** (1), pp. 155-164.

PETRONIO C., DI CANZIO E. & SALARI L. (2007) - *The Late Pleistocene and Holocene Mammals in Italy: new biochronological and paleoenvironmental data.* Palaeontographica Abteilung A, **279** (4-6) , pp. 147-157.

RAVAZZI C. (2003) - *An overview of the quaternary continental stratigraphic units based on biological and climatic events in Italy*. Il Quaternario - Volume Speciale INQUA,**16**(1Bis), pp. 11-18.

RIO D., SPROVIERI R., CASTRADORI D. & DI STEFANO E. (1998) - *The Gelasian Stage (Upper Pliocene): A new unitnof the global standard chronostratigraphic scale.* Episodes, **21** (1), pp. 82-87.

ROOK, L., MART›NEZ-NAVARRO, B. & HOWELL, C. F. (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**, pp. 267–277.

RUDDIMAN, W F, RAYMO, M E, MARTINSON, D G, CLEMENT, B M,& BACKMAN, J. (1989) - *Pleistocene evolution: northern hemisphere ice sheets and North Atlantic Ocea.* Paleoceanography, **4**, pp. 353–412.

SABATO L., BERTINI A., ALBIANELLI A., NAPOLEONE G. & PIERI P. (2005) - *The lower and middle pleistocene geologic record of the San Lorenzo lacustrine succession in the Sant'Arcangelo Basin (Southern Apennines, Italy).* Quaternary International, **131**, pp. 59–69.

SALA B. (1992) - *I mammiferi del Quaternario italiano. In: Tugnoli, C. (Ed.), I segni del tempo - Memoria*

delle origini ed icone del primordiale. Atti del corso di aggiornamento per personale docente, Trento, pp. 209–227.

SALA B. (2005) - *Mammalian faunas and environment from the Würmian Glacial Maximum of the Italian peninsula (approx. 22±2 ka cal BP).* Annali dell'Università degli Studi di Ferrara, Museologia Scientifica e Naturalistica, spec. vol. 2005, pp. 125- 129.

SALA B. & MASINI F. (2007) - *The late Pliocene and Pleistocene small mammal chronology in the Italian peninsula.* Quaternary International, **160** (1), pp. 4-16.

SALA B., MASINI F., FICCARELLI G., ROOK L. & TORRE D. (1992) - *Mammal dispersal events in the Middle And Late Pleistocene Of Italy And Water Europe*. Courier Forsch.-Inst. Seckenberg, **153**, Pp. 58-68

SALA B., MASINI F., FICCARELLI G., ROOK L. & TORRE D. (1992) - *Mammal dispersal events in the Middle and Late Pleistocene of Italy and Water Europe*. Courier Forschungs-Instituts Senckenberg, **153**, pp. 58–68.

SALVADOR A. (1994) - *International Stratigraphic Guide. A Guide to Stratigraphic Classification, Terminology, and Procedure,* 214 pp., The Geological Society of America, Boulder

SARDELLA R. & PALOMBO M.R. (2007) - *What significance for the Wolf event?* Quaternarie, **18** (1), pp. 65-71

SCHENCK, H.G. & MULLER, S.W. (1941) - *Stratigraphic terminology.* Geological Society of America Bulletin, **52**, pp. 1419–1426.

SCHOCH R.M. (1989) - *Stratigraphy: Principles and methods*. Van Nostrand Reinhold, New York, 375 pp.

SHACKLETON N.J. (1997) - *The Deep-Sea Sediment Record and the Pliocene-Pleistocene Boundary.* Quaternary International, **4**, pp.33-36.

SPASSOV N. (2003) - *The Plio–Pleistocene vertebrate fauna in South-Eastern Europe and megafaunal migratory waves from the east of Europe*. Revue de Paléobiologie, **22** (1), pp. 197–229.

SUC J.-P. & POPESCU S.M. (2005) - *Pollen records and climatic cycles in the North Mediterranean region since 2.7 Ma.* In HEAD M J. & GIBBARD P.L. (Eds): Early-Middle Pleistocene transitions: the land-ocean evidence. Geological Society of London, Special Publication, **24**, pp. 147–158.

SUC J.P., BERTINI A., LEROY S.A.G., & SUBALLYOVA D. (1997) - *Towards the Lowering of the Pliocene/Pleistocene Boundary to the Gauss/Matuyama Reversal.* Quaternary International, **40**, pp. 37-42.

TEDFORD, R.H. (1970) - *Principles and practices of mammalian geochronology in North America.* American Paleontology Convenction Chicago, Lawrence, KS: Allen Pres, **1969,** Part. F, pp. 666-703.

TEICHERT, C. (1958) - *Some biostratigraphical concepts.* Geological Society of America Bulletin, **69**(1), pp. 9–120.

TORRE D. (1987) - *Pliocene and Pleistocene marine-continental correlations*. Ann. Inst. Geol. Publ. Hung, **70**, pp. 71-77

TORRE D., ALBIANELLI A., BERTINI A., FICCARELLI G., MASINI F. & NAPOLEONE G. (1996) - *Paleomagnetic calibration of Plio–Pleistocene mammal localities in central Italy.* Acta Zoologica Cracoviensia, **39** (1), pp. 559–570.

TORRE D., FICCARELLI G., MASINI F., ROOK L.& SALA B. (1992) - *Mammal dispersal events in the Early Pleistocene of Western Europe.* Courier Forschungs-Institut Senckenberg, **153**, pp. 51–58.

TRIANTIS K.A., MYLONAS M., LIKA K. & VARDINOYANNIS K. (2003) - *A model for the species–area–habitat relationship.* Journal of Biogeography, **30**, pp. 19–27.

WALSH S.L. (1998) - *Fossil datum and paleobiological event terms, paleontostratigraphy, chronostratigraphy, and the definition of Land Mammal "Age" boundaries.* Journal of Vertebrate Paleontology, **18** (1), pp. 150-179.

WILLIAMS, H.S. (1901) - *The discrimination of time values in Geology.* Journal of Geology, **9** (7), pp. 570–585.

ZAGWIJNW.H. (1974) - *The Pliocene-Pleistocene boundary in western and southern Europe*. Boreas, **3**, pp. 75-97.