

BIOCHRONOLOGY OF PLIO-PLEISTOCENE MAMMALIAN FAUNAS ON THE ITALIAN PENINSULA: KNOWLEDGE, PROBLEMS AND PERSPECTIVES

Maria Rita Palombo

Dipartimento di Scienze della Terra, Università "La Sapienza"
CNR- Istituto di Geologia Ambientale e Geoingegneria
Piazzale A. Moro, 5 I-00185 ROMA, Italy <mariarita.palombo@uniroma1.it>

ABSTRACT: Palombo M.R., *Biochronology of Plio-Pleistocene Mammalian Faunas on the Italian Peninsula: Knowledge, Problems and Perspectives*. IT ISSN 0394-3356, 2004

The biochronological setting thus far proposed for mammalian faunas from the Italian peninsula (constructed on the basis of classic criteria: the absence/presence of particular taxa, faunal turnovers, the "evolutionary stage" of taxa belonging to a well-defined phyletic lineage or "typical taxa associations") provides a highly-detailed categorization of Italian assemblages. Nevertheless, the more detailed the bioevent sequence becomes, the more difficult it is to establish correlations on a larger scale. Multivariate analysis (the recognition of successive, non-overlapping, ecologically-adjusted assemblages of taxa living together in a given space and time) may provide a useful tool for defining faunal complexes having broader biochronological significance. As far as Middle Pliocene- Middle Pleistocene large mammalian faunas from the Italian peninsula are concerned, on the basis of our results, we operationally consider the following complexes as possible high-rank biochrons: Villafranchian+ early Galerian (Middle, Late Pliocene +Early Pleistocene local faunal assemblages) = "Archaic Faunas Complex" (AFC), and middle, late Galerian+early Aurelian (Middle Pleistocene) = "Modern Faunal Complex" (MFC). Moreover, the following groups may be regarded as possible lower-rank biochrons: I = early Villafranchian; II = middle Villafranchian + late Villafranchian; III = latest Villafranchian + early Galerian; IV = middle and late Galerian; V = early Aurelian. The separation between the two main clusters highlights the faunal renewal occurring during the latest Early Pleistocene, as confirmed by mammalian species turnover and richness trends. The important reorganization of faunal complexes, characterising the transition from the late Villafranchian plus early Galerian (Early Pleistocene) to the middle-late Galerian plus early Aurelian (Middle Pleistocene) mammalian faunas, can be linked to worsening climate during the last part of the Early Pleistocene (from about 1.1 to about 0.8 Ma). This evidence encourages reconsideration of the definition of Galerian Land Mammal Age (LMA) previously proposed for Italian mammalian faunas.

The definition of biochronology (the method most widely-applied to the terrestrial realm in order to relate biological events to the geological time scale), whose application has often been tainted by reference to and inference from biostratigraphy, is briefly reconsidered.

RIASSUNTO: Palombo M.R., *Biocronologia dei complessi faunistici a grandi mammiferi del Plio-Pleistocene della penisola italiana: problemi, conoscenze, prospettive*. IT ISSN 0394-3356, 2004.

L'assetto biocronologico fin ad ora proposto per i complessi a grandi mammiferi dalla penisola italiana si basa essenzialmente su bioeventi di comparsa e scomparsa e quindi sui classici criteri di assenza/presenza di definiti taxa, rinnovi faunistici, "grado evolutivo" di taxa appartenenti a ben definite linee filetiche, riconoscimento di "associazioni tipiche". Gli schemi attualmente in uso forniscono una scansione biocronologica dettagliata dei complessi faunistici italiani, tuttavia, quanto maggiore è la quantità di dati di nuovo acquisizione e quanto più dettagliata diviene la sequenza bioeventi riconosciuti, tanto più difficile risulta operare correlazioni a grande scala. Le analisi multivariate (finalizzate alla definizione di "gruppi" di faune locali tra loro ben discriminabili, ciascuno dei quali costituente un insieme di taxa presumibilmente vissuti in uno stesso intervallo temporale in definite aree geografiche, coerente dal punto di vista ecologico) possono fornire un mezzo utile di indagine per una prima definizione di complessi faunistici che abbiano una più ampia valenza biocronologica. I risultati ottenuti per complessi faunistici a grandi mammiferi della penisola italiana dal Pliocene medio al Pleistocene medio, con analisi di somiglianza e di ordinamento dei bioeventi, suggeriscono di considerare quali biochroni di più alto rango due complessi faunistici: il complesso "Villafranchiano + Galeriano inferiore" (local faunal assemblages, LFAs, del Pliocene medio e superiore e del Pleistocene inferiore), qui denominato "complesso faunistico arcaico" (AFC), e il complesso "Galeriano medio e superiore + Aureliano inferiore" (LFAs del Pleistocene medio), qui denominato "complesso faunistico moderno" (MFC). Inoltre, possono essere considerati quali possibili biochroni di rango inferiore i seguenti gruppi: I = Villafranchiano inferiore; II = Villafranchiano medio + Villafranchiano superiore; III = tardo Villafranchiano superiore + Galeriano inferiore; IV = Galeriano medio e superiore; V = Aureliano inferiore. La separazione fra i due gruppi principali evidenzia il profondo rinnovamento faunistico che si realizza alla fine del Pleistocene inferiore. La riorganizzazione dei complessi a grandi mammiferi, che caratterizza la transizione tra il complesso che riunisce le LFAs del tardo Villafranchiano e del Galeriano inferiore (Pleistocene inferiore) e quello delle LFAs del Galeriano medio, superiore e dell'Aureliano inferiore (Pleistocene medio), può essere correlata con il deterioramento climatico del tardo Pleistocene inferiore (da circa 1,1 a circa 0,8 Ma). Su queste basi, sembrerebbe, quindi, auspicabile una ridefinizione dell'Età a mammiferi (Land Mammal Age, LMA) "Galeriano", come a suo tempo proposta per le faune a mammiferi della penisola italiana. Vengono anche brevemente discussi la definizione di biocronologia ed i suoi criteri di applicazione.

Keywords: Biochronology, Pliocene, Pleistocene, Large Mammals, Italy.

Parole chiave: Biocronologia, Pliocene, Pleistocene, Grandi Mammiferi, Italia.

1. FOREWORD

As claimed by Lindsay (2003), chronostratigraphy (the method generally applied to the oceanographic-marine realm) and biochronology (that most commonly applied to the terrestrial realm), are the prime conceptual methods for relating biological events to the geological time scale. Nevertheless, to date, the organisation of geological time on the basis of evidence supplied by continental mammal faunas has continued to be a field plagued by interpretative and semantic confusion.

The divergence of opinions on biostratigraphic/biochronological matters may often be attributed to interference between operational (based on stratigraphic records like biostratigraphy) and theoretical (based on bioevents linked to taxa evolution and palaeocommunity transformation - biochronology) methodological approaches (see e.g. Tedford, 1970; Mein 1975, 1990, 1998; Woodburne, 1977, 1987, 1996; Berggren and Van Couvering, 1978; Guerin, 1982, 1990; De Giuli *et al.*, 1983; Daams & Freudenthal, 1981; Flynn *et al.*, 1984; Lindsay, 1985, 1997, 2001, 2003; Archibald *et al.*, 1987; Emry *et al.*, 1987; Krishtraika *et al.*, 1987; Lindsay & Tedford, 1990; Pickford, 1990; Fernandez-Lopez, 1991; Brujin *et al.*, 1992; Lister, 1992; Lucas, 1992; Salvador, 1994; Berggren *et al.*, 1995a, 1995b; Prothero, 1995; Opdyke *et al.*, 1997; Sen, 1997; Van Dam, 1997, 2001, 2003; Daams *et al.*, 1998; Fejfar *et al.*, 1998; Walsh, 1998; Agusti *et al.*, 2001; Azanza *et al.*, 2002; Koufos, 2003; Ravazzi, 2003 etc). Moreover, even if biochronology is a fundamental tool in correlating terrestrial deposits, "biochronology has never been discussed in any stratigraphic code because of that loose and ambiguous application" (Lindsay, 2003 p.216). However, it is worth noting that a biochronological unit is a time span defined by palaeobiological events, while a biostratigraphic unit is a body of rock strata defined by its fossil content (stratigraphic datum) (Schoch, 1989; Salvador, 1994). Indeed, discontinuity in the continental sedimentary record, the rarity of deposits formed in a regime of virtually continuous sedimentation, the anisotropy of palaeoenvironmental conditions and taphonomic and sampling biases are responsible for the fact that the stratigraphic order of the highest and lowest occurrences (stratigraphic datum) of taxa remains within a given geographical area does not necessarily reflect the temporal order of their actual first/last appearances (palaeobiological events) in time.

Therefore, as far as large continental mammals are concerned, given that: 1) the actual occurrence in time of a palaeobiological entity (both in general or in a given geographical area) cannot be unquestionably established by its fossil evidence; 2) the relative or absolute deposition dates for rock-bodies in which the first/oldest and last/youngest local appearances of fossil remains (lowest and highest stratigraphic records) are documented, respectively correspond only to the "ante quem" or "post quem" time of actual origination and extinction bioevents; 3) boundaries (specific surfaces within a sequence of rock strata selected as the standard for defining and recognising biostratigraphic units, Salvador, 1994) are not indicative "because of the impossibility of defining them with precision" (Gliozzi *et al.*, 1997, p.369) and "biozones" ("bodies of rock strata

that are defined or characterised on the basis of their contained fossils", Salvador, 1994, pag. 53) cannot be defined, even if "biochrons" have previously been regarded as similar to "concurrent range" or "assemblage" zones (Gliozzi *et al.*, 1997). Ultimately, biochronology can be defined as "the organization of geologic time according to the irreversible process of organic evolution" (Lindsay, 2003). "Biochrons" represent lapses of time during which faunas demonstrate clear taxonomic homogeneity (see also Alberdi *et al.*, 1997); from an operational point of view, they might be considered as "blocks of coordinated stasis" (Brett *et al.*, 1996) during which no turnover is expected. Faunal complexes belonging to biochrons may be regarded as non-overlapping and "ecologically adjusted groups of animals with specific geographic limits and chronologic range" (Tedford, 1970, pag. 602).

Nonetheless, if on the one hand first/last appearance bioevents (palaeobiological events on which biochronology is based) have been the principal basis for establishing the chronological setting of continental mammalian faunas, on the other hand these bioevents are documented by the lowest/highest occurrences of fossil remains in fossiliferous levels of various continental stratigraphic successions (stratigraphic datum, the basis of biostratigraphy). Indeed, mammalian paleostratigraphy (*sensu* Walsh, 1998) is actually founded on fossil records available in continental rocks, and new discoveries can substantially alter pre-established biochronological schemes.

The biochronological settings thus far proposed for mammal faunas on the Italian peninsula have been based on the faunal complexes named faunal units (FUs), further classified in a number of Land Mammal Ages (LMAs). The definition of FUs derives from bioevents, such as the first appearance of one or more taxa, and/or the possible disappearance of others on the evolutionary stage, displayed by taxa belonging to a well-established phyletic lineage, or on typical taxa associations. This substantially agrees with Lindsay's definition (2003) for LMAs, defined as relatively short intervals of geologic time that can be recognized and distinguished from earlier and later units (in a given region or province) by a characterising assemblage of mammals.

Since initial introduction of these biochrons (Azzaroli, 1977), Italian palaeontologists have proposed some new FUs and/or new Mammal Ages (MAs) or revised others (see e.g. Torre, 1987; Sala *et al.*, 1992; Caloi & Palombo, 1996; Gliozzi *et al.*, 1997; Petronio & Sardella, 1999; Palombo *et al.*, 2004). The introduction of such new biochrons often depends on acquiring new data and discovering new fossiliferous assemblages that enable better discrimination of the temporal succession of bioevents by means of the highest and lowest occurrences in local sedimentary sequences. Indeed, the complex physiography of the Italian Peninsula, the geographical and ecological barriers represented by the Alpine and Apennine chains, together with its remarkable latitudinal rather than longitudinal extension, as well as the great influence of the Mediterranean Sea on climatic conditions, supply a unique opportunity to analyse the influence of various factors influencing the structure of mammal assemblages in the course of time. It is thus evident that the current biochronological sche-

me provides very detailed resolution for Italian assemblages, but is less useful for comparing and correlating other European mammal faunas.

The aim of this paper is: 1) to provide a concise picture of our knowledge of biochronology of Italian large mammals; 2) to update previous biochronological schemes in light of the latest discoveries; 3) to define adjusted homogeneous groups of taxa having biochronological significance using multivariate analyses; 4) to compare these "groups" with previously-established biochrons.

2. BIOCHRONOLOGICAL FRAMEWORK: AN OVERVIEW

To define the chronological framework of Italian mammal faunas, a number of schemes have been proposed by several authors (for instance Ambrosetti *et al.*, 1972; Azzaroli, 1977, 1982, 1983, 1991; De Giuli *et al.*, 1983; Torre, 1987; Azzaroli *et al.*, 1988; Torre *et al.*, 1992, 1996; Caloi & Palombo, 1990, 1996; Gliozzi *et al.*, 1997; Petronio & Sardella, 1999). Initially, Azzaroli (1977) proposed a subdivision of six FUs for mammal faunas belonging to the Villafranchian LMA. Subsequently, the discovery of new faunas, adding to knowledge of faunal renewal phases and the transitional character of some local assemblages (LFA), led to the introduction of new faunal units and/or new proposed mammal ages. In 1997, Gliozzi *et al.* suggested a biochronological scheme for Middle Pliocene to Late Pleistocene Italian continental faunas (large and small mammals, fresh-water molluscs and brackish ostracods) that has recently been widely utilised by Italian palaeontologists. Three LMAs were defined for the time span between the Middle Pliocene and Late Pleistocene: Villafranchian (late Middle Pliocene to early Early Pleistocene), Galerian (late Early Pleistocene to early Middle Pleistocene), and Aurelian (late Middle Pleistocene to Late Pleistocene), respectively including eight (Triversa, Montopoli, Saint Vallier, Costa San Giacomo, Olivola, Tasso, Farneta, Pirro), four (Colle Curti, Slivia, Isernia, Fontana Ranuccio) and more than two FUs (Torre in Pietra, Vitinia and non-defined). Moreover, the transitional character of some local faunas was pointed out (see discussion in Gliozzi *et al.*, 1997). Subsequently, Petronio & Sardella (1999) proposed Ponte Galeria local fauna as representative of a distinct middle Galerian FU, transitional to Isernia FU.

2.1 The Villafranchian Land Mammal Age (LMA)

The Villafranchian was originally defined as an Age/Stage, since Pareto (1865) designated the lower boundary of the Villafranchian stratotype in Villafranca d'Asti (Italy) at the bottom of the vertebrate bearing fluvio-lacustrine sequence overlying Pliocene marine beds. Subsequently, the "Villafranchian" question has been extensively debated (see Carraro, 1996 for a review and discussion). However, subsequent authors considered the Villafranchian as a biochron/biochronozone defined by dispersal events, and not as a geochron/geochronozone, formally defined by golden spikes. For example, Heintz (1970) considered the Villafranchian as a biochron including the Middle and Late Pliocene. This French scientist divided his

Villafranchian into four biochrons (early, middle, late and latest Villafranchian) on the basis of taxa belonging to phyletic lines of cervid taxa. On the other hand, Azzaroli (1977) extended the Villafranchian to the Early-Middle Pleistocene boundary. More recently, Gliozzi *et al.* (1997) considered the Villafranchian MA a biochron beginning with faunal turnover marked by the appearance of newcomers such as "*Pseudodama*" (= *Axis* according to Di Stefano & Petronio, 2003), *Leptobos stenometopon*, and *Stephanorhinus elatus* (= *S. jeanvireti*), and ending before the Jaramillo Subchron.

2.1.1 Early and middle Villafranchian FUs

Based on faunal renewals, the Villafranchian LMA was divided into early, middle and late sub-biochrons (Azzaroli *et al.*, 1988; Gliozzi *et al.*, 1997).

The early Villafranchian is represented by the Triversa FU, established on a number of local faunas from the Villafranca d'Asti area (Piedmont) and from central Italy (e.g. Lower and Upper Valdarno, Arcille, Spoleto). Palaeomagnetic analysis at Fornace R.D.B. (Villafranca d'Asti) ascribes the sequence to Gauss Chron (Lindsay *et al.*, 1980). Nevertheless, according to Lindsay *et al.* (1995), the intervals of reversed magnetic polarity separated by a normal magnetozone previously identified at Fornace R.D.B. cannot be correlated with the Mammoth or Khaena episodes, but with the late Gilbert Chron. Nevertheless, this hypothesis disagrees with geological palynological evidence (Albianelli *et al.*, 1995, 1997; Bertini & Roion, 1997) as well as with the paleomagnetic calibration (Torre *et al.* 1996) carried out on a long sedimentary sequence containing typical early Villafranchian fossil assemblages appearing at the Santa Barbara quarry (lignitic lacustrine silty clays and sands, Meleto clays from the Castelnuovo dei Sabbioni sequence, Upper Valdarno). The results attest a long normal polarity interval interrupted a few meters above the fossiliferous lignite level by a reversed polarity interval, respectively attributable to the late Gauss age and the short Kaena event. Consequently, the beginning of the early Villafranchian can be dated at about 3.3-3.2 Ma. B.P.

The Triversa faunal complex (Table 1), although renewed with respect to Ruscinian faunas, maintained quite a damp forest character: pachyderms and small-middle sized Ruscinian *Perrissodactyla* and *Artiodactyla*, mainly browsers or mixed-feeders inhabiting dense or clear woodland, were still present, along with arboreal omnivores such as *Ursus minimus*. On the other hand, the disappearances of primates and carnivores inhabiting humid and forest environments, as well as the appearance of some taxa dwelling in more or less open environments, such as *Leptobos stenometopon*, testified to moderate structural renewal, which can be correlated with the climatic cooling taking place at about 3.2/3.1 (Palombo, 2004).

The following Montopoli FU is based on the rich fauna from a site near Montopoli (Lower Valdarno), found in a fossiliferous level at the top of a marine sequence, calibrated with the Gauss/Matuyama transition (Lindsay *et al.*, 1980). The Montopoli local faunal assemblage (LFA), (dated to about 2.6 Ma), as well as the Montopoli F. U., have long been considered Early Villafranchian in age. Nevertheless, the noticeable faunal turnover characterising the transition from the

Triversa F.U. to the Montopoli F.U., delineated by the cooling event taking place about 2.6/2.5 Ma, may be regarded as a bioevent marking the beginning of the Middle Villafranchian (Alberdi *et al.*, 1998, Caloi & Palombo 1999, Palombo 1995, 2004, Palombo *et al.*, 2003).

The reorganization of "palaeocommunities" from the early to middle Villafranchian (the so-called "Elephant-*Equus* event" *sensu* Lindsay *et al.*, 1980), corresponds to a true turnover and can be regarded as the starting point of a dispersal phase. In the Montopoli FU, forest taxa greatly diminished and several new herbivores appeared, including large-sized ones and pachyderms, such as a primitive *Mammuthus* (see Palombo & Ferretti, 2005 for a discussion). Moreover, the occurrence of the large *Equus livenzovensis* was consistent with the increasing extension of grassy areas, characterised by herbaceous vegetation of the steppe type, suggesting arid conditions (Suc *et al.* 1995; Torre *et al.* 2001; Palombo, 2004).

Italian faunal assemblages belonging to the middle Villafranchian ("Saint Vallier" FU) are scanty, with weak stratigraphic constraints. For example, the Colle Pardo LFA (Anagni basin, Cassoli & Segre Naldini, 2000), despite the scarcity of faunal remains, has been considered intermediate in age between the Montopoli and Costa San Giacomo complexes by several authors (Caloi & Palombo, 1996; Gliozzi *et al.*, 1997). According to the faunal list, only the occurrence of a Caprinae (possibly similar to *Hemitragus orientalis* recorded at the Late Pliocene Bulgarian site of Slivnitsa, Cregut-Bonnoeur & Spassov, 2003) might exclude attribution to an older faunal complex (?Montopoli FU). Consequently, using only large mammals, a faunal complex characterising the "Saint Vallier" FU cannot be adequately defined in Italy, unless running through taxa are considered.

In the following Costa San Giacomo FU, a dog, similar to the late Villafranchian species *Canis etruscus*, and *Sus strozzi* were first recorded (Costa San Giacomo LFA, Anagni basin, Biddittu *et al.* 1979). Moreover, typical middle Villafranchian taxa, such as "*Pseudodama*" *lyra* (*Axis lyra*, according to Di Stefano & Petronio, 2003), *Eucladoceros tegulensis*, *Leptobos merlai*, *Gazella borbonica* and *Gazellospira torticornis* were still present, along with the Ruscinian- middle Villafranchian taxon *Anancus arvernensis*¹.

The diffusion of the genus *Canis* in Europe, the so called "wolf event" (*sensu* Azzaroli, 1983) [*Canis* sp. is also recorded at Chilhac (Monguillon-Douillet, 2000), a site dating more than 1.9 Ma (Bœuf, 1997)], possibly a more gradual phenomenon than previously supposed, crossed the Plio-Pleistocene boundary (*sensu* Aguirre & Pasini, 1985)² and culminated at the beginning of the Pleistocene, at the time of the Tasso FU.

2.1.2 The Beginning of the late Villafranchian

The faunal renewal taking place at the end of the Late Pliocene involved both carnivore and herbivore guilds, which clearly became more diversified. Most Pliocene species disappeared, particularly among herbivores, and new carnivores and herbivores progressively spread across the Italian peninsula (Table 1). Thus this renewal may be regarded as an increasing dispersal phase rather than an actual turnover (Palombo,

2004).

According to Azzaroli (1977), three FUs (Olivola, Tasso and Farneta) belong to the late Villafranchian, at that time considered to coincide with the early Pleistocene. Subsequently, a fourth FU, Pirro, more advanced than Farneta, was added (Caloi & Palombo, 1996), and the end of the late Villafranchian was later brought forward, before the Jaramillo Subchron (Gliozzi *et al.*, 1997).

The LFA from Olivola (Val di Magra) is characterised by the lowest occurrence of *Pachicrocuta brevirostris*, *Panthera gombazsoegensis*, "*Pseudodama*" *nestii* (*Axis nestii* according to Di Stefano & Petronio, 2003) and *Eucladoceros dicranios*; scanty remains of *Procambptoceras brivatense* were also found, whereas *Canis etruscus* was represented by several individuals.

Two late Villafranchian LFAs, Matassino and Casa Frata, were retrieved from the Upper Valdarno, from fossiliferous levels cropping out along the Montevarchi sequence (Borselli *et al.*, 1980; De Giuli & Masini, 1987). Matassino and Casa Frata LFAs were ascribed respectively to Olivola and Tasso FUs (Azzaroli *et al.*, 1988; but see Gliozzi *et al.*, 1997), due the occurrence of new taxa such as *Lycaon falconeri* (see Martinez Navarro & Rook, 2003, for a discussion) at Casa Frata, *Equus stehlini*,? *Lepobos vallisarni* and *Praeovibos* sp. Moreover, Matassino and Casa Frata LFAs have been respectively calibrated with the β event and with the top of the Olduvai Subchron (Torre *et al.*, 1996). Recently, a new faunal assemblage was collected at Poggio Rosso, in sediments of the second deposition phase called the Montevarchi Succession (*Argille del Torrente Ascione*, Albanelli *et al.*, 1995; Mazza *et al.* 2004), just below the Plio-Pleistocene boundary, but about 30 m above the Matassino LFA (Napoleone *et al.*, 2001; Napoleone & Azzaroli, 2002; Napoleone *et al.*, 2003). The taxonomical composition of the Poggio Rosso LFA is "intermediate" between that of Olivola and Tasso FUs due to, for example, the occurrence of both *Canis arvensis* and *Chasmaporthetes lunensis* (Mazzini *et al.*, 2000; Mazza *et al.*, 2004). Accordingly, on the basis of magnetostratigraphic calibration of the Matassino and Poggio Rosso localities, the late Villafranchian theoretically started during the latest Pliocene, undoubtedly before the Plio-Pleistocene boundary. According to Napoleone

¹ It is worth noting that Zanchetta & Mazza (1996) proposed an Early Pleistocene age for a fragmentary skeleton of *Anancus* from Monte Castello (Lower Valdarno); in any case, this datum requires confirmation.

² The profuse changes in flora and fauna during this event have prompted several authors (Alberdi *et al.* 1997; Suc *et al.* 1997; Morrison & Kukla, 1998 and references therein) to propose placing the Plio-Pleistocene boundary here. [We have to note that, as pointed out by Kofschoten & Gibbard (1998, p. 16) "the fact that the Vrica boundary was only notified by the Moscow IGC in 1984, should not be a reason for not reconsidering the boundary position". Thus, the lowering of the Pliocene/Pleistocene boundary to around the Gauss/Matuyama palaeomagnetic reversal (MIS 104, approximately 2.6 Ma) is being debated by several authors, as well as the INQUA Commission of Stratigraphy. In this paper, we provisionally maintain the Plio-Pleistocene boundary proposed by Aguirre & Pasini (1985), even if the global change occurring at MIS 104 should be considered a more appropriate boundary.

et al. (2003, p. 308), faunas belonging to the Olivola FU could be “inferred as pre-Olduvaiian, not younger than 2.0 Ma.”

Moreover, it is worth noting that the structure of faunal complexes ascribed to Olivola and Tasso FUs are not very dissimilar, the second differing essentially in the appearance of *Lycaon falconeri*, *Leptobos vallsarni* and *Equus stehlini*, whereas *Galgogoral meneghini* and *Gazellospira torticornis* were not recorded. Moreover, the *Hippopotamus antiquus* from Valdarno, whose appearance was previously considered as belonging on the Tasso FU, was probably retrieved from fossiliferous levels younger than those of the Monteverdichi succession (Napoleone *et al.*, 2003). Accordingly, the Olivola and Tasso faunal complexes seem to express the same progressive faunal renewal culminating with the “Tasso” faunal complex. Consequently, the hypothesis that the Olivola and Tasso faunal complexes may represent a single FU cannot be definitively ruled out.

2.2 The End of the Villafranchian LMA and the Dawn of the Galerian LMA

During the following Early Pleistocene (“Postgalerian” *sensu* Caloi & Palombo, 1996), most of the typical Villafranchian taxa disappeared or became rare, and some new species, phylogenetically linked to taxa characterising early Middle Pleistocene faunas, progressively appeared. On the whole, during the Early Pleistocene (late Villafranchian *pro parte* and early Galerian), herbivores inhabiting open environments became more abundant, and forest dwellers noticeably reduced their diversity (Table 1). This is consistent with the Early Pleistocene climatic trend, characterised by a progressive decrease in mean temperature, although climatic oscillations were not accentuated. Moreover, several data suggest the spread of grassland/steppe areas (Suc *et al.*, 1995; Bertini, 2000 and references therein). *Equus stenonis* was replaced by the slender-limbed *Equus altidens* and by the heavier, larger equid already ascribed to the problematic group of *Equus bressanus/Equus suessenbornensis*. Among pachyderms, rhinoceroses, perhaps linked to *Stephanorhinus hundsheimensis*, seem to have been ecological substitutes for *Stephanorhinus etruscus*. Moreover, ovibovines, *Megalovis* sp., and *Bison*-like bovines appeared locally (*Bison (Eobison) degiuli* and perhaps another taxon (?*Bison* sp.) may be linked to the more advanced middle Galerian *Bison schoetensacki*). Nevertheless, forest areas were still rather abundant and, little by little, woodlands spread during more temperate and humid climatic phases. Woodlands were mainly inhabited by cervids belonging to the small-medium sized species of the “*Pseudodama*” genus and by the larger mixed-feeder “*Praemegaceros*” *obscurus*³, which replaced the browser *Eucladoceros* (Table 1).

Furthermore, a number of data seem to confirm the transitional character of typical late Villafranchian and Galerian mammal assemblages (Azzaroli *et al.*, 1988, Caloi & Palombo, 1996; Palombo, 2004 and references therein).

According to Gliozzi *et al.* (1997), the appearance of “*Praemegaceros*” *verticornis* is the bioevent conventionally marking the beginning of the Galerian LMA (Colle Curti FU). The lowest species occurrences of

this taxon in Italy is in the Colle Curti LFA, calibrated with the Jaramillo Subchron (Coltorti *et al.*, 1998). However, Colle Curti LFA shares several taxa (carnivores, rhinoceros, hippopotamuses) with older LFAs belonging to the Pirro Nord FU (Table 1). Thus, despite the appearance of “*Praemegaceros*” *verticornis* as well as the innovative characteristics demonstrated by arviculids from Colle Curti LFAs (Coltorti *et al.*, 1998), early Galerian LFAs seem more closely related to the latest Villafranchian faunas than to ensuing true Galerian ones (Palombo *et al.*, 2003; Palombo, 2004; Palombo & Valli, 2004).

The end of the Early Pleistocene (end of the Villafranchian event *sensu* Azzaroli *et al.*, 1988) actually represented the most significant period of striking faunal renewal on the Italian peninsula, giving rise to remarkable palaeocommunity reorganization involving faunal migrations and extinction events (see Alberdi *et al.* 1997, Gliozzi *et al.* 1997; Palombo, 2004; Palombo *et al.*, in press).

2.2.1 Middle and late Galerian Faunal Complexes

The middle Galerian (early Middle Pleistocene) came into being during great climatic cooling (stages 24 and 22 of the marine oxygen isotopic signal, MIS) characterising the beginning of the Middle Pleistocene (*sensu* Cita & Castradori, 1995)⁴.

Faunal renewal derives from two distinct trends: 1) the progressive reduction in richness characterising late Early Pleistocene faunas (from Farneta to Colle Curti FUs), 2) the subsequent dispersal and progressive diffusion in Italy of taxa from Eastern and Central Europe, leading to an important and relatively rapid increase in diversity (Slivia FU) (Palombo, 2004).

³ The name *Megaceroides* (type species “*Cervus*” *algericus* Lydekker 1890) was proposed by Joleaud in 1914, as a *Cervus* subgenus for a fragmentary maxillary; subsequently, Arambourg (1932, 1938) ascribed a skull from the Late Pleistocene of Algeria and Morocco to this species. Similarities in skull features between specimens from the Magreb and the megacerines (= Megacerini tribus, *sensu* Viret 1961) from Europe, first pointed out by Azzaroli (1952), have subsequently been widely debated (see e.g. Hadjoudis, 1990; Azzaroli & Mazza, 1992; Croitor, 2004; Abbazzi, in prep.). All in all, it seems more correct to maintain the name *Megaceroides* only for the North African species. Nevertheless, the problem concerning the nomenclature of the genera referring to the tribe Megacerini is still unresolved. Assuming that the species ascribed to the so-called “verticornis” group and the “giganteus” group belong to two distinct lineages, what is the correct generic name among those used thus far for the giant deer belonging to the “verticornis” group and the “giganteus” group belong to two distinct lineages, what is the correct generic name among those used thus far for the giant deer belonging to the “verticornis” group? The name “*Praemegaceros*”, though not formally correct (see e.g. Azzaroli, 1979; Caloi & Palombo, 1996), has been frequently employed, whereas other names, such as “*Ortognoceros*” or “*Psekupsoceros*”, have not been *de facto* utilised in more recent times. For this reason, to avoid additional confusion, we provisionally use the generic name “*Praemegaceros*” for these giant European deer.

⁴ It is worth noting that the Early- Late Pleistocene boundary is currently placed informally at the Matuyama/Brunhes palaeomagnetic inversion (Richmond 1996), but Cita & Castradori (1995) proposed a lower horizon at Marine Isotope Stage (MIS) 25.

In the course of time (Table 1), the appearances of several pachyderms (*Elephas (Palaeoloxodon) antiquus*, *Mammuthus trogontherii*, *Stephanorhinus kirchbergensis*, *Stephanorhinus hemitoechus*), cervids (small-sized *Capreolus capreolus*, medium-sized *Cervus elaphus* and *Dama clactoniana*, large-sized *Megaloceros savini* and “*Praemegaceros*” *solihacus*) and large and middle-sized bovines (*Hemibos galerianus* - see Martinez Navarro & Palombo 2004, for a discussion-, *Bos primigenius*, *Ovis ammon antiqua* and *Hemitragus bonali*), brought about a major change in herbivore guilds. Among carnivores, *Crocota crocuta* was surely recorded for the first time in the Ponte Galeria 2 LFA (Sardella, 2004), whereas the lowest occurrence of some other large carnivores (active hunters that were both flesh-eaters and scavengers, such as *Ursus deningeri*, *Panthera pardus*, *Panthera leo fossilis*, and “*Hyaena prisca*”) was even later, in LFAs belonging to the Isernia FU.

According to Gliozzi *et al.* (1997), two FUs, Slivia and Isernia, belong to this mammal subLMA. Subsequently, Petronio & Sardella (1999) proposed a new FU, Ponte Galeria FU, based on specimens found in HST deposits of the PG2 sedimentary sequence cropping out along the Latium coast (= Ponte Galeria 2, see Milli *et al.*, 2004). The above-mentioned authors believed the age and taxonomical composition of the Ponte Galeria FU to be intermediate between the Slivia and Isernia LFAs. If the three middle Galerian FUs were valid, they would differ essentially in the persistence of *Mimomys savini*, *Pachycrocuta brevirostris* and *Panthera gombaszoegensis* (Slivia FU), the exclusive occurrence of *Hemibos galerianus* (Ponte Galeria FU) and the appearance of *Bos primigenius* (Isernia FU). Nevertheless, it is possible that Slivia and Ponte Galeria 2 LFAs belong to the same FU due to the uncertain identification of some herbivores from Slivia local fauna, as well as limited knowledge of the carnivores and micromammals from the Ponte Galeria 2 LFA (Palombo, 2004). Moreover, an arvicolid similar to *Mimomys savini* has recently been found in Pagliare di Sassa LFA (L'Aquila, Abruzzo) (Palombo and Di Canzio, unpublished data) where “*Praemegaceros*” *verticornis*, *Megaloceros savini* (as in Ponte Galeria) and *Dama* cf. *D. clactoniana* were also recorded (Palombo *et al.*, 2001).

As far as the transition from the middle (Isernia FU) to the late Galerian (Fontana Ranuccio FU) is concerned, we can place it around 500 ka, in view of the age proposed for the LFAs ascribed to the Isernia FU (Notarchirico, estimated age about 600 ka, Lefèvre & Raynal 1999, Lefèvre *et al.* 1999; Isernia, estimated age about 600 ka; Coltorti *et al.*, 2000), and the possible age of the Fontana Ranuccio LFA (estimated age about 458 ka, Biddittu *et al.* 1979).

During the late middle Galerian (Fontana Ranuccio FU), “Villafranchian” taxa had not been recorded and the number of very large herbivores diminished (Table 1), leaving the occurrence of “Galerian” equids and megacerines in doubt. Moreover, the specialised and slightly larger *H. antiquus* was replaced by *Hippopotamus amphibius* and, among carnivores, *Ursus arctos* appeared, as well as *Felis silvestris silvestris* (Table 1).

2.3 Early Aurelian Faunal Complexes

Gliozzi *et al.* (1997) proposed the Aurelian LMA (divided into early, middle and late Aurelian) for late Middle (from 10 to 6 MIS) and Late Pleistocene mammal faunas (from 5 to 1 MIS). The authors separated the early and middle Aurelian on the basis of faunal differences between Torre in Pietra and Vitinia FUs (Caloi & Palombo 1990, 1996), whereas no characteristic FUs have been designated for the late Aurelian.

The Vitinia FU was considered dissimilar to the Torre in Pietra FU, essentially due to the abundance of a primitive fallow deer (*Dama dama tiberina*) and the appearance of *Cervus elaphus*, with features similar to those of modern forms of red deer and *Equus hydruntinus* (Caloi & Palombo, 1996; Gliozzi *et al.* 1997). Both these FUs have been defined on the basis of palaeontological and stratigraphic data collected in the Campagna Romana area (cfr. Caloi *et al.*, 1998 and references therein). Nevertheless, the structure and taxonomical composition of Torre in Pietra and Vitinia faunal complexes are similar (Palombo & Mussi, 2001; Palombo 2004), so the division into two FUs seems to be based on weak palaeontological evidence. Moreover, it is worth noting that the LFA of Sedia del Diavolo (Rome) referred to the Vitinia FU, since the abundance of *Dama dama “tiberina”* remains were found in alluvial deposits overlaying “Tufo lionato” (dated 355 ka by Karner *et al.*, 2001), where *Equus hydruntinus* was also found (Caloi & Palombo, 1995). Caloi *et al.* (1998) correlated the Sedia del Diavolo deposits containing *Dama dama “tiberina”* remains with the Vitinia Formation (MIS 7). Nonetheless, on top of the deposits previously correlated with MIS 7, an ash flow deposit, dated 285 ± 1 ka by Karner *et al.* (2001), has been recognised (Marra & Rosa, 1995). In conformity with this new chronological data, the deposition of the fluvio-lacustrine sediments overlaying “Tufo lionato” at Sedia del Diavolo occurred approximately between 355 and 285 ka (Palombo *et al.*, 2004). Accordingly, *Dama dama “tiberina”* and *Equus hydruntinus* were already present during MIS 9, and thus the Vitinia FU cannot be considered a valid biochron. The LFAs previously ascribed to the Torre in Pietra and Vitinia FUs must be included in a single FU (named Torre in Pietra FU for reasons of priority). Several bioevents characterised the beginning of this FU, as well as the beginning of the Aurelian LMA (subdivided into early and late Aurelian): *Canis lupus* and *Felis silvestris silvestris* first appeared, as well as *Ursus spelaeus*, substituting *U. deningeri*, and *E. hydruntinus*, *Megaloceros giganteus*, *Dama dama “tiberina”*, and *Bubalus* (Palombo, unpublished data), whereas *Ovis ammon antiqua* and *Bison schoetensacki* were not yet recorded (Table 1).

3. IN SEARCH OF NEW BIOCHRONOLOGICAL ASSESSMENTS

In recent years, several multivariate approaches have been developed in an attempt to supplement the similarity and association concepts. Actually, multivariate analysis, if not conclusive in itself, can be a useful tool in initially defining faunal complexes and could be used to limit the biochronological framework based on classic methodologies (Azanza *et al.*, 1997, 1999;

Palombo *et al.*, 2003 and references therein). In order to quantify the similarities and biochronological relationships among selected local mammal assemblages and establish a faunal succession, we have applied two different kinds of multivariate analysis: "appearance event ordination" (AEO; Alroy, 1994) and similarity cluster analysis (see e.g. Hazel, 1970).

The former method uses the various relationships between the first and last appearances of taxa (actually the highest and lowest occurrences of their fossil remains in local faunas) as basic data. Chronological information is inferred by detecting which taxa appear before the last occurrence of another one. The "best" solution in this procedure involving correspondence analysis is to search for a parsimonious arrangement of events that minimises the overall number of implied first and last appearance relationships. "Appearance event ordination" is based on parsimony, as only relationships between first and last "appearances" in several LFAs are taken into account, while occurrences of common taxa are not considered (see Palombo *et al.*, 2003, for a discussion).

In the second method, the presence of common taxa provides basic data for evaluating similarities between local faunas grouped according to their taxonomic homogeneity. Conversely, the absence of a species, highly dependent on taphonomic and random factors, supplies no precise information. We evaluated similarities on the basis of the Jaccard binary coefficient and cluster analysis performed using the UPGMA method, as according to this method each member of a cluster has equal weight at all levels of clustering (cfr. Hazel 1970; Shi 1993; Azanza *et al.*, 1997, 1999; Palombo *et al.*, 2003 and references therein) (NTSYS-PC program, version 2.0, Rohlf, 1998). Clusters do not necessarily supply chronological information or necessarily imply recognition of successive, non-overlapping, ecologically-adjusted assemblages of taxa living together in a given space and time. For this reason, the Q-Mode dendrogram, particularly suitable for biochronologically-oriented studies (cfr. Hazel 1970), was preferred.

3.1 "Appearance Event Ordination"

Calibration of the appearance event sequence (Fig. 1) introduces a temporal distortion that becomes greater as available dating diminishes, as in the case of Italian faunas. The distortion between the actual and estimated ages of localities indicates a contraction in time for Ruscinian and early+middle Villafranchian LFAs (from 4.5 to 2.5 Ma) and quite good correspondence for late Villafranchian and Galerian (2.0 to 0.400 Ma), whereas early Aurelian LFAs are dated more recently (between 0.400 and 0 Ma) (see Azanza *et al.*, 2004).

After obtaining chronological relationships for Italian mammal faunas, two groups can be identified, corresponding to the Pliocene + Early Pleistocene and to the Middle Pleistocene LFA (Fig. 1).

Within the first group, early Villafranchian LFAs appear equivalent in age, whereas the middle Villafranchian are distributed in a span of less than 1 Ma, in accordance with the faunal renewal characterising this faunal complex. Colle Pardo LFA is shown to be older than the Montopoli LFA, probably due to the absence of *Mammuthus* and *Equus* in the former loca-

lity. The distribution of LFAs ascribed to Olivola and Tasso FUs confirms the homogeneity within each faunal complex, as well as the intermediate evolutionary stage of the Poggio Rosso LFA. Matassino cannot be clearly positioned, given the scarcity of biochronologically-relevant taxa. Successive LFAs are arranged according to the progressive renewal characterising the late Early Pleistocene.

Within the group including Middle Pleistocene LFAs, Slivia and Ponte Galeria LFAs appear to be the most archaic among middle Galerian faunas, whereas Fontana Ranuccio and Visogliano (late Galerian) undergo the greatest change, along with Valdemino, which actually belongs to the middle Galerian, but where some taxa (such as *Panthera pardus* and *Bos primigenius*) were recorded for the first time on the Italian peninsula (Nocchi & Sala, 1997).

The reduced biochronological significance of some late Middle Pleistocene (early Aurelian) LFAs makes it impossible to define their relationships. We can note that Paglicci (external beds) and Torrente Conca LFAs set a part, probably because of the occurrence of *Rupicapra* and *Capra ibex* (the latter only in the Paglicci LFA).

3.2 Similarities between LFAs

Among large mammal faunas from the Middle Pliocene to the late Middle Pleistocene, 74 LFAs were selected for a new similarity analysis, improving and updating those already performed on Italian mammal LFAs (Palombo *et al.*, 2003; Palombo 2004; Palombo & Valli, in press). The faunal list for each locality was critically reviewed, including up-to-date records and personal observations. Since Italian FUs are in some cases based on the appearance of subspecies, these taxa were also included in the data matrix.

The Q-mode dendrogram (Fig. 2) separates local faunal assemblages (LFAs) into two main groups and reveals a major separation between Pliocene-Early Pleistocene (cluster A = Villafranchian LMA and early Galerian, Colle Curti FU) and Middle Pleistocene LFAs (cluster B = middle, late Galerian - Slivia, Isernia and Fontana Ranuccio FUs-, and early Aurelian, Torre in Pietra FU), the latter group having a rather higher similarity coefficient.

The major separation between A and B clusters underlines the faunal reorganisation which occurred during the climatic crisis taking place at the Early to Middle Pleistocene transition (*sensu* Cita & Castradori, 1995). This renewal phase seems to have been more important than those marking transitions from the early to the middle Villafranchian (the so-called "Elephant-*Equus* event" *sensu* Lindsay *et al.*, 1980) and from the middle to the late Villafranchian (the so-called "wolf event" *sensu* Azzaroli, 1983).

A and B clusters share a low number of taxa; consequently, we can hypothesize that each one makes up part of "an ecologically adjusted group of animals with specific geographic limits and chronological range" (Tedford 1970: 602). Alberdi *et al.* (1997) have informally named these kinds of aggregates "Superages", considering them equivalent to "Chronofauna" (*sensu* Tedford 1970, Emry *et al.*, 1987). We informally name these groups "Archaic Faunal Complex" (AFC = cluster A) and "Modern Faunal Complex" (MFC = cluster B).

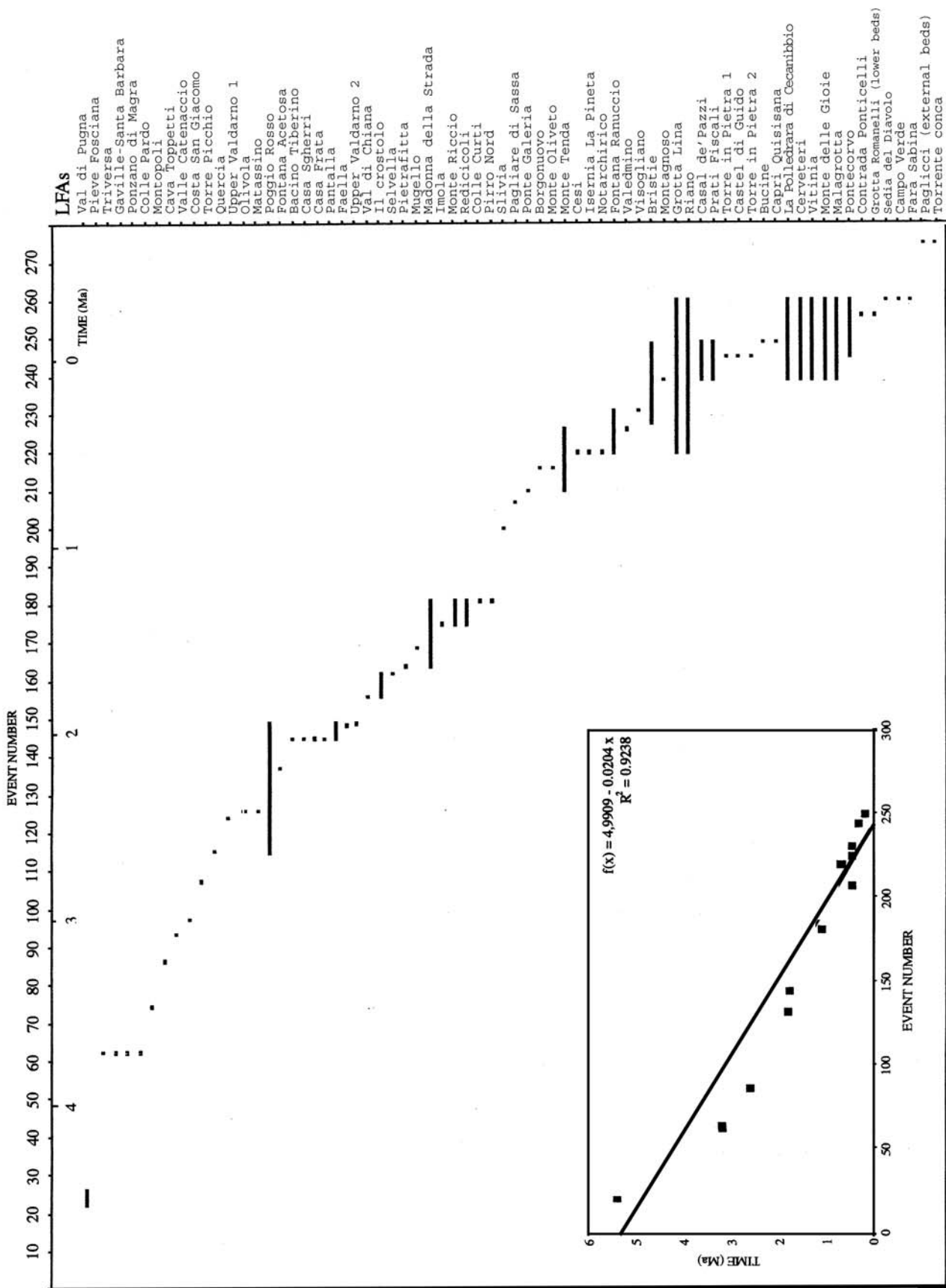


Fig.1 - Chronological relationships for Italian mammal faunas ordered according to a "parsimony-based approach" (Appearance event ordination, Alroy 1992, 1994). Ordinalmento biochronologico delle faune locali della Pliocene medio al Pleistocene medio utilizzando il metodo "Appearance event ordination" di Alroy (1992, 1994).

Both clusters are further divided into subclusters; within A, A₁ includes early Villafranchian (Triversa FU) LFAs as well as the Ruscian Val di Pugna LFA (included to indicate the age pole in the analysis, see Bianucci *et al.* 2001), whereas A₂ includes middle and late Villafranchian LFAs, as well as early Galerian ones.

Accordingly, the separation between Triversa and Montopoli FUs seems to be the most significant within the AFC, emphasising the importance of the transition from early to middle Villafranchian (an important turnover phase) with respect to that from the middle to late Villafranchian (prevalently a dispersal phase) (Palombo, 2004).

Within the A₂ subcluster, a gap separates the A_{2.1} group, including middle + early late Villafranchian LFAs (from Montopoli to Tasso FUs), from the A_{2.2} group including the latest Villafranchian + early Galerian LFAs (from Farneta to Colle Curti FUs).

Actually, early late Villafranchian complexes (Olivola and Tasso FUs) were relatively static and quite homogeneous; moreover, the presence of long-persistent and frequent middle Villafranchian taxa (such as *Mammuthus meridionalis*, *Stephanorhinus etruscus* and *Equus stenonis*) can explain their greater resemblance to middle Villafranchian LFAs than to subsequent latest Villafranchian ones. An extinction phase followed, during which last occurrences surpassed new ones. This phase culminated at the Pirro/Colle Curti FU transition with a moderate turnover, due to the appearance in the course of time of some new taxa typical of the Middle Pleistocene (Table 1). A minor gap separates the group of LFAs belonging to the Farneta FU from the group of Pirro and Colle Curti FUs, thus pointing out the strong similarities between latest Villafranchian and early Galerian Italian LFAs. Actually, Pirro Nord and Colle Curti LFAs show a relatively high similarity coefficient (Jaccard index = 0.3), due to the presence of several common taxa (carnivores, rhinoceros, hippopotamus) in both localities. This fact markedly reduces the importance of the occurrence of "*Praemegaceros*" *verticornis* in the Colle Curti LFA.

Within cluster B, including Middle Pleistocene LFAs, group B₁ stands apart, probably because the FLAs included share few taxa with other middle and late Galerian LFAs due to low richness (Borgo Nuovo, Monte Oliveto, Pagliare di Sassa) or the occurrence of peculiar taxa, such as *Mammuthus meridionalis* in the Monte Tenda LEA and *Hemibos galerianus* in the Ponte Galeria LFA.

Within B₂, group B_{2.1} includes middle and late Galerian LFAs. The Valdemino LFA shows a low similarity coefficient and stands apart from the other LFAs, probably due to the occurrence of *Panthera pardus*, not recorded in other Italian Galerian LFAs, and the generic identification of some taxa such as *Ursus* sp.

Group B_{2.1} includes LFAs attributed to the Torre in Pietra FU (e.g. La Polledrara, Castel di Guido, Malagrotta, Sedia del Diavolo, Torre in Pietra lower level, correlated with MIS 9 and Vitinia, Casal de' Pazzi, Torre in Pietra upper level correlated with MIS 7), although it is difficult to justify the clustering of groups of minor rank, probably because of the basic homogeneity of this faunal complex.

On the basis of our results and taking into account both the biochronological significance of some

rare taxa and the influence of long-lived ones, we will operationally consider clusters A and B as high rank biochrons (A = "Archaic Faunas Complex" AFC, and B = "Modern faunal complex" MFC) and the following groups as possible biochrons of lower rank: I = early Villafranchian (A₁); II = middle Villafranchian + late Villafranchian (A_{2.1}); III = latest Villafranchian + early Galerian (A_{2.2}); IV = middle and late Galerian (B₁); V = early Aurelian (B₂) (Fig. 2). In addition, the two groups of middle (A_{2.1.1}) and early late Villafranchian (A_{2.1.2}) should also be regarded as possible biochrons due to their low similarity coefficient.

4. REMARKS

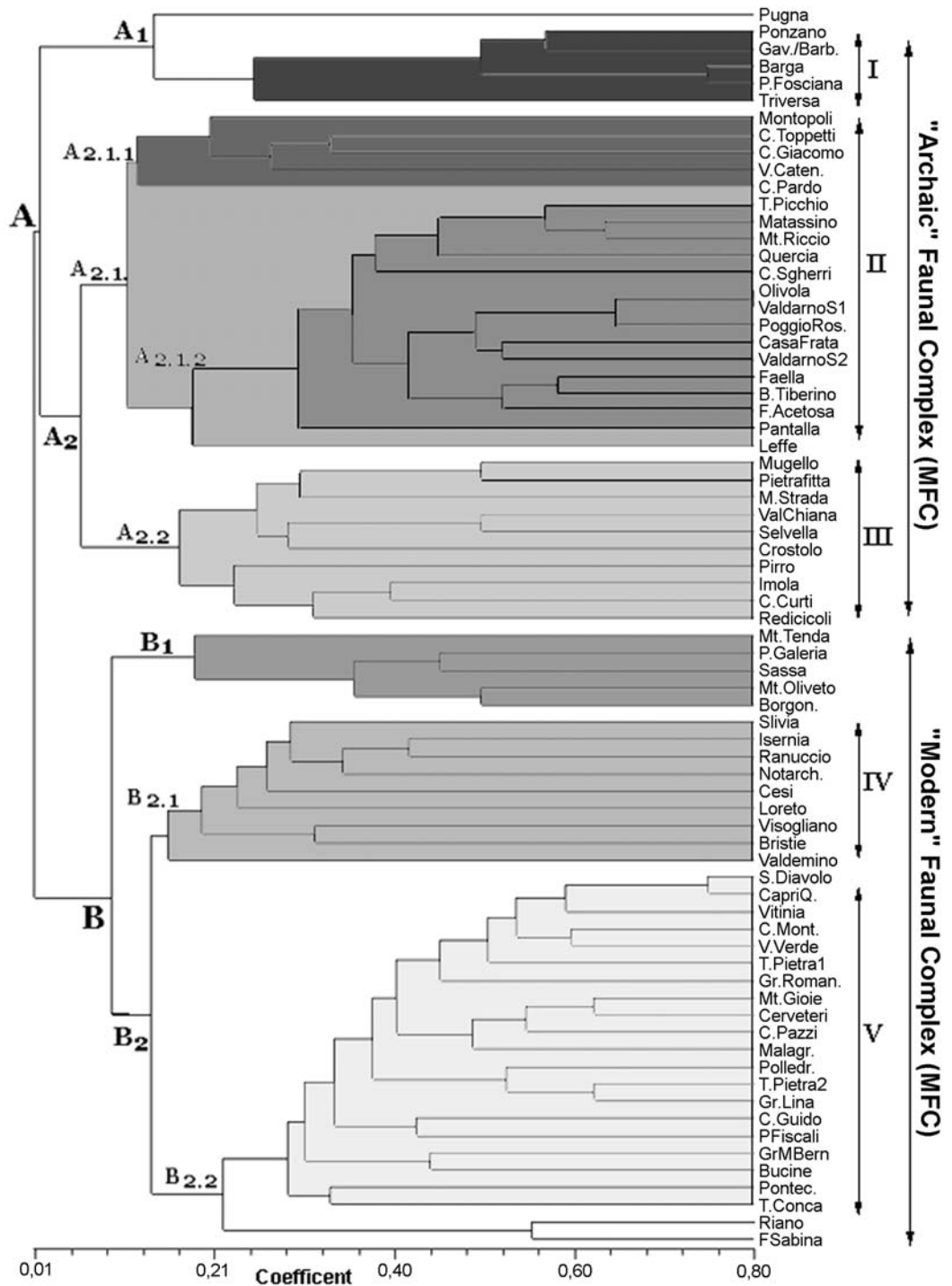
The transition from Early to Middle Pleistocene faunas (from early to middle Galerian MAs, *sensu* Gliozzi *et al.* 1997), coinciding with the onset of 100 ka climate cyclicity and vegetational changes, represents major community reorganisation in the Western Mediterranean area (see e.g. Azanza *et al.*, 1999, in press; Palombo & Valli, in press; Palombo *et al.*, in press and references therein). The importance of this renewal and ecological reorganisation is highlighted by the clear separation between clusters of "archaic" (Villafranchian + early Galerian, Middle Pliocene and Early Pleistocene) and "modern" (middle, late Galerian + early Aurelian, Middle Pleistocene) Italian mammal faunas, as well as by the AEO. This change results from a moderate turnover, taking place at the Pirro-Colle Curti FU transition, followed by marked faunal renewal at the beginning of the Middle Pleistocene.

This evidence encourages reconsideration of the definition of Galerian Land Mammal Age (LMA) previously proposed for Italian mammalian faunas. Indeed, as mentioned above, according to Gliozzi *et al.* (1997), the appearance of "*Praemegaceros*" *verticornis*, first recorded in Italy in the Colle Curti LFA, conventionally marks the beginning of the Galerian LMA. However, this fauna seems more similar to Villafranchian than to ensuing "true" Galerian LFAs, and the renewal between Colle Curti and Slivia FUs was more significant than that between Pirro and Colle Curti FUs (Table 1; Fig. 3). Moreover, and as far as large Italian mammals are concerned, analysis results confirm that during the late Pliocene and Pleistocene, the most important faunal renewals (due both to originations /immigrations and extinctions) are linked to major global climatic changes.

Faunal renewal ("elephant-*Equus* event", Lindsay *et al.*, 1980; Azzaroli 1983; Azzaroli *et al.*, 1988) from the early to middle Villafranchian faunal complexes, linked to Pliocene climate worsening, is responsible for the slight similarity between A₁ and A₂ subclusters. This renewal may be regarded as a true turnover phase due to the high percentage of last and new appearances and the important ecological structural change in faunal complexes, involving both herbivore and carnivore guilds. Moreover, this event may be considered the starting point of a dispersal phase leading to a progressive standing richness increase during the following Pliocene and up to the beginning of the Early Pleistocene, given that new occurrences exceeded last occurrences (Fig. 3).

On the other hand, even if the so-called "wolf-

Fig. 2 - Dendrogram Q-Mode for 74 Italian local faunal assemblages (Q-mode) based on un-weighted data for 136 taxa. CCC = 0.92936. Abbreviations: Pugna= Val di Pugna; Ponzano= Ponzano di Magra; Gav/Barb.= Gaville Santa Barbara; P. Fosciana= Pieve Fosciana; C.Toppetti= Cava Toppetti; C.Giacomo= Costa San Giacomo; V.Caten= Valle Catenaccio C. Pardo= Colle Pardo; T.Picchio= Torre Picchio; Mt.Riccio= Monte Riccio; C.Sgherri= Casa Sgherri; Valdarnos1= Upper Valdarno 1; PoggioRos= Poggio Rosso; Valdarnos2= Upper Valdarno 2; B. Tiberino= Bacino Tiberino; F.Acetosa= Fontana Acetosa; M.Strada= Madonna della Strada; Val Chiana = Val di Chiana; Pirro = Pirro Nord; C.Curti = Colle Curti; Mt.Tenda= Monte Tenda; P. Galeria = Ponte Galeria; Sassa = Pagliare di Sassa; MtOliveto = Monte Oliveto; Borgon. = Borgonuovo; Isernia = Isernia la Pineta; Ranuccio = Fontana Ranuccio; Notarch. = Notarchirico; Loreto = Venosa-Loreto; S.Diavolo = Sedia del Diavolo; CapriQ. = Capri-Quisisana; Vitinia = Vitinia, upper levels (MIS 7); C.Mont. = Contrada Monticelli; C.verde = Campo Verde; T.Pietra1 = Torre in Pietra, lower levels (MIS 9); Gr.Rom. = Grotta Romanelli, lower levels; Mt.Gioie = Monte delle Gioie; CPazzi = Casal de' Pazzi; Malagr. = Malagrotta; Polled. = La Polledrara di Ceganibbio; T.Pietra2 = Torre in Pietra, upper levels (MIS 7); GrLina = Grotta Lina; CGuido = Castel di Guido; PFiscali = Prati Fiscali; GrMBern. = Grotta Maggiore di San Bernardino; Pontec. = Pontecorvo; T.Conca = Torrente Conca; FSabina = Fara Sabina.



Dendrogramma Q-Mode ricavato per 74 faune locali italiane (Q-mode) sulla base dell'analisi di 136 taxa. CCC = 0.92936. Abbreviazioni: Pugna= Val di Pugna; Ponzano= Ponzano di Magra; Gav/Barb.= Gaville Santa Barbara; P. Fosciana= Pieve Fosciana; C.Toppetti= Cava Toppetti; C.Giacomo= Costa San Giacomo; V.Caten= Valle Catenaccio C.Pardo= Colle Pardo; T.Picchio= Torre Picchio; Mt.Riccio= Monte Riccio; C.Sgherri= Casa Sgherri; Valdarnos1=Upper Valdarno 1; PoggioRos= Poggio Rosso; Valdarnos2= Upper Valdarno 2; B.Tiberino= Bacino Tiberino; F.Acetosa= Fontana Acetosa; M.Strada = Madonna della Strada; Val Chiana = Val di Chiana; Pirro = Pirro Nord; C.Curti = Colle Curti; Mt.Tenda = Monte Tenda; P.Galeria = Ponte Galeria; Sassa = Pagliare di Sassa; MtOliveto = Monte Oliveto; Borgon. = Borgonuovo; Isernia = Isernia la Pineta; Ranuccio = Fontana Ranuccio; Notarch. = Notarchirico; Loreto = Venosa-Loreto; S.Diavolo = Sedia del Diavolo; CapriQ. = Capri-Quisisana; Vitinia = Vitinia, upper levels (MIS 7); C.Mont. = Contrada Monticelli; C.verde = Campo Verde; T.Pietra1 = Torre in Pietra, lower levels (MIS 9); Gr.Rom. = Grotta Romanelli, lower levels; Mt.Gioie = Monte delle Gioie; CPazzi = Casal de' Pazzi; Malagr. = Malagrotta; Polled. = La Polledrara di Ceganibbio; T.Pietra2 = Torre in Pietra, upper levels (MIS 7); GrLina = Grotta Lina; CGuido = Castel di Guido; PFiscali = Prati Fiscali; GrMBern. = Grotta Maggiore di San Bernardino; Pontec. = Pontecorvo; T.Conca = Torrente Conca; FSabina = Fara Sabina.

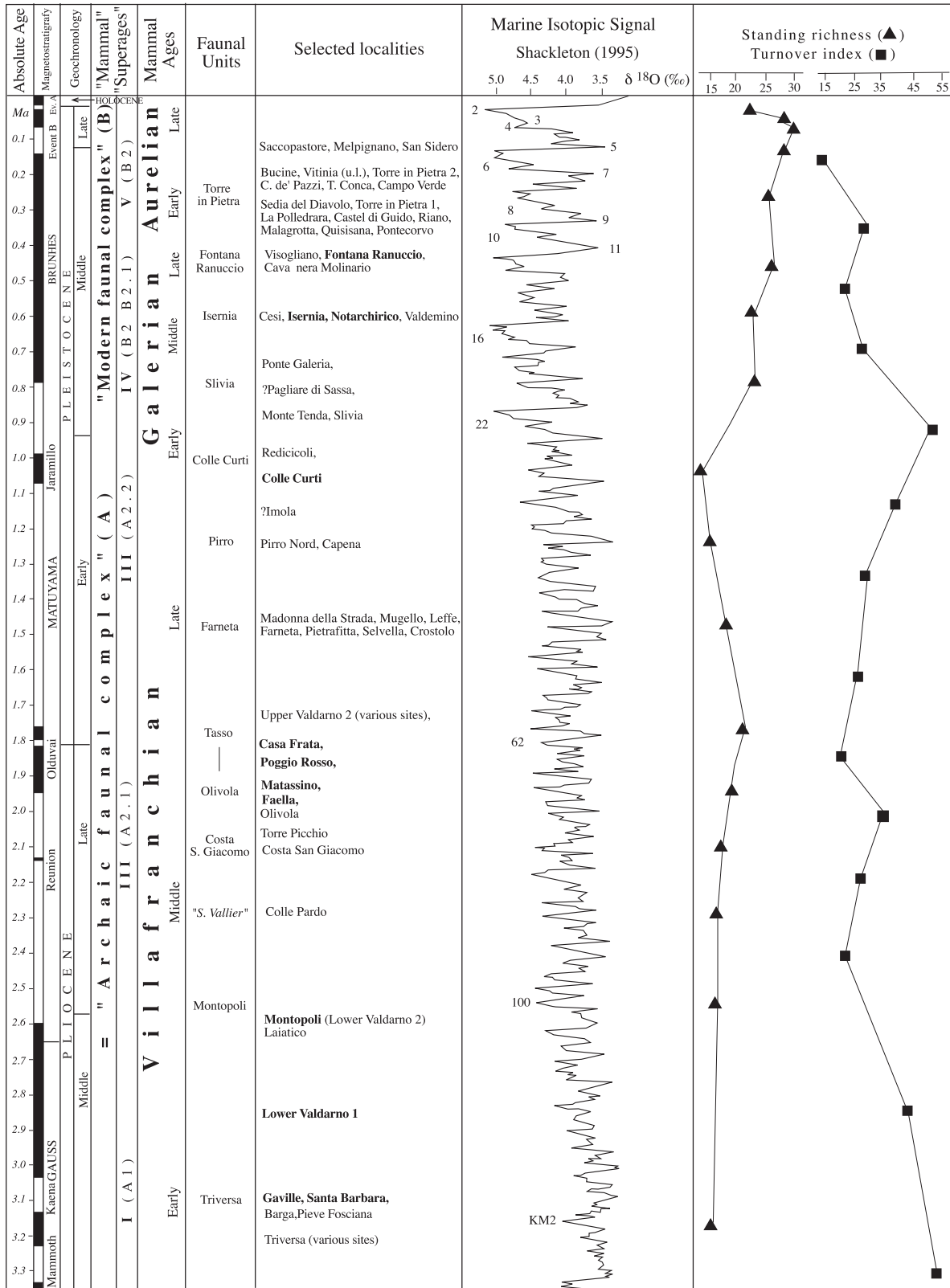


Fig. 3 – Biochronology, standing richness and turnover changes of Italian large mammal faunas from Middle Pliocene to Late Pleistocene. Standing richness value was calculated according to Harper’s method (Harper, 1975) ($N_{sr} = N_{bda} + N_{rt} + 1/2 (N_f + N_{l-} - N_o)$) where N_{sr} = number of taxa that potentially occur at a given time interval, N_{bda} = number of species present before-during and after the faunal unit, N_{rt} = number of species present before and after but not in the faunal unit, N_f = number of first appearances, N_{l-} = number of last appearances, N_o = number of taxa present only in the faunal unit). Faunal renewal was evaluated considering all occurrences at the transition between two successive FUs (turnover index, $TI = \% FA + \% LA / 2$ as in Torre et al., 1999).
Biocronologia, ricchezza standardizzata e rinnovi faunistici delle faune a grandi mammiferi della penisola italiana dal Pliocene medio al Pleistocene superiore. La ricchezza standardizzata è stata calcolata secondo la formula proposta da Harper (1975): $N_{sr} = N_{bda} + N_{rt} + 1/2 (N_f + N_{l-} - N_o)$; N_{sr} = numero pesato dei taxa presenti nell'intervallo considerato, N_{bda} = numero di specie presenti prima, durante e dopo l'intervallo considerato, N_{rt} = numero dei taxa presenti prima e dopo, ma non durante l'intervallo di tempo considerato, N_f = numero delle prime comparse, N_{l-} = numero delle ultime comparse, N_o = numero dei taxa presenti solo nell'intervallo considerato. L'indice di rinnovo è stato calcolato valutando il numero totale di taxa, le prime comparse e le scomparse alla transizione tra due successivi intervalli, secondo la formula $TI = \% FA + \% LA / 2$ come in Torre et al. (1999).

event" (Azzaroli 1983, Azzaroli *et al.*, 1988), seems to be a more gradual phenomenon than previously supposed, middle Villafranchian LFAs and early late Villafranchian LFAs form separate groups within A_{2,1}, clearly separated from the group including late Early Pleistocene LFAs, in which taxa phylogenetically related to or identical to Galerian Middle Pleistocene ones progressively appeared, while "Pliocene species" were no longer present.

Finally, similarity analysis results confirm the basic homogeneity of late Middle Pleistocene LFAs. Consequently, without stratigraphic constraints it is difficult to arrange these assemblages in a chronological sequence that is ascribing them to a specific MIS.

Given these considerations, the biochronology of Plio-Pleistocene Italian mammal faunas should be re-evaluated, taking the following factors into account:

- "biochrons" represent time lapses during which faunas have a degree of taxonomic homogeneity; the "faunal complex" belonging to each biochron might be regarded as non-overlapping and an "ecologically adjusted group of animals with specific geographic limits and chronological range" (Tedford, 1970, pag. 602);
- actually, biochronology, a theoretical discipline, operationally depends on the empirical documentation of the stratigraphic ranges of fossils in superimposed sections;
- relative or absolute deposition dates for rock-bodies in which fossil remains are first/last documented respectively correspond only to the "ante quem" or "post quem" time of actual origination and extinction bioevents;
- the more detailed the bioevent sequence becomes, the more difficult it is to make correlations on a larger scale;

Moreover, the application of multivariate analysis may be a useful tool in defining faunal complexes having a high degree of similarity. Since separation between clusters corresponds to faunal renewal, clusters themselves should have biochronological significance and should be taken into consideration for biochronological correlations.

On the basis of the results obtained, the faunal complex corresponding to LFAs previously ascribed to FUs from Farneta to Colle Curti should be considered as the most advanced biochron in the Villafranchian LMA; accordingly, the beginning of the Galerian LMA must correspond to the faunal reorganization occurring at the Early to Middle Pleistocene transition.

Moreover, the validity and applicability of lower rank biochrons resulting from our multivariate analysis (I = early Villafranchian, Triversa FU; II = middle Villafranchian + late Villafranchian, from Montopoli to Olivola + Tasso FUs; III = latest Villafranchian + early Galerian, from Farneta to Colle Curti FU; IV = middle and late Galerian, from Slivia to Fontana Ranuccio FU; V = early Aurelian, Torre in Pietra FU) need further confirmation.

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