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Villafranchian: The long story of a Plio-Pleistocene European large mammal biochronologic unit

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ABSTRACT

European continental mammal biochronology has been developed in Italy since the pioneering work of Augusto Azzaroli. The Villafranchian is a Mammal Age, a biochronological unit. Biochronology is a subdivision of geological time on the basis of the succession of evolutionary stage of faunal assemblages and dispersal events. The Villafranchian Mammal Age is based on European large mammals and corresponds, in the International Stratigraphic Scale, to a time span from Late Pliocene to most of the Early Pleistocene. Within these limits the Villafranchian spans from around 3.5 Ma to about 1.0–1.1 Ma. "Villafranchian" is a concept relatively common within the scientific literature of continental stratigraphers in Europe. Unfortunately, it is sometimes used in the wrong way or in wrong contexts, especially because the term Villafranchian has been used with the meaning of a continental stage, totally misunderstanding its significance as a biochronologic unit. The authors provide an update of the Villaranchian Mammal Age and its present significance.

1. Introduction: historical review of the Villafranchian Mammal Age, a biochronologic unit

Vertebrate paleontologists subdivide geological time using biochronological scales based on the succession of evolutionary stage of faunal assemblages and dispersal events, the Mammal Ages *sensu* Lindsay (1990); see also Tedford (1970), Woodburne (1977), Guérin (1990), Lindsay and Tedford (1990), Lindsay (2003). The European continental mammal biochronology was developed in the 1960s and 1970s thanks to the pioneering work of eminent vertebrate paleontologists including Emile Heintz and Pierre Mein in France and Augusto Azzaroli (Fig. 1) in Italy.

The Mammal Age Villafranchian is a biochronological unit based on large mammals spanning the interval from Late Pliocene to most of the Early Pleistocene in Europe. "Villafranchian" is a concept of widespread use within the scientific community of continental stratigraphers in Southern Europe. Unfortunately, it sometimes used in the wrong way or in incorrect contexts.

The term Villafranchian was proposed by Pareto (1865) as a continental stage referring to fluvial and lacustrine sediments in the surroundings of Villafranca d'Asti (Piedmont) that contained remnants of mammal fauna. The same author also included within the Villafranchian definition mammalian faunas from Upper and Lower Valdarno basins, in Tuscany. It was generally considered to represent the youngest part of the continental Pliocene. Gignoux (1916) proposed a correlation of this stage with his marine Calabrian, the latter assumed at that time to represent the late Pliocene. In 1948, at the 18th International Geological Congress held in London, it was agreed to place the Calabrian at the base of the Pleistocene and consequently, the Villafranchian was also considered to represent the earliest stage of the continental Pleistocene. Some authors (Azzaroli, 1962, 1970) remarked however that the so-called "Villafranchian mammal assemblages" were not homogeneous, nor strictly contemporary.

A first attempt to subdivide "Villafranchian" mammal assemblages is probably detectable in the early 1960s pioneering works of Howell (1959), Bout (1960, 1967), Bourdier (1961) and Azzaroli (1962). In the following years, both Heintz (1968, 1970), Heintz et al. (1974) and Azzaroli (1970), Azzaroli and Vialli (1971) proposed a comparable structured sub-division of the Villafranchian. The chronological sub-division of the Villafranchian was thus extensively discussed during two meetings in 1975 and 1976 (Azzaroli, 1977; Alberdi and Aguirre, 1977). As a result, a number of successive faunal units (Azzaroli, 1977, 1983 originally described six) were recognized subdividing the Villafranchian into Early, Middle and Late Villafranchian. In the International Stratigraphic Scale,[1] the

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[1] Although still contested within the Quaternarist community (cfr Van Couvering et al., 2009; McGowran et al., 2009), we follow here the recent formal IUGS recognition (June 2009) of Quaternary as a Period/System with the redesignation of the base of the Pleistocene Series/Epoch in the 2.59 Ma GSSP of the Gelasin Stage.

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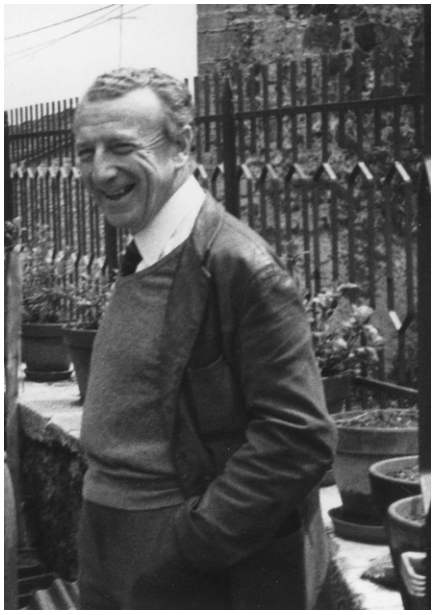

Fig. 1. Augusto Azzaroli in the mid 1970s. Photo courtesy of E. Cioppi.

Early Villafranchian corresponds to the Late Pliocene from ~3.5 to ~2.6 Ma (the former Middle Pliocene), the Middle Villafranchian to the early part of the Early Pleistocene (Matuyama pre-Olduvai subchron), from ~2.6 to ~2.0 Ma (most of the former Late Pliocene), and the Late Villafranchian covers most of the rest of the Early Pleistocene (Matuyama from Olduvai to Jaramillo subchrons), a time span from ~2.0 to ~1.0 (that includes the latest part of the former Late Pliocene to most of the former Early Pleistocene). Within these limits the Villafranchian spans from around 3.5 Ma to about 1.0–1.1 Ma (Fig. 2). During this long time interval, remarkable faunal changes took place. The term Villafranchian has come to lose much of its intrinsic value (Azzaroli, 1977) and its name is maintained for historical reasons and for the sake of stability in nomenclature, but has no real meaning unless it is used with definite qualification: early Villafranchian, middle Villafranchian, and late Villafranchian, or better with the indication of a definite faunal unit (Azzaroli, 1992).

Until the mid-1980s, most references to the Villafranchian implied correlations (direct or indirect) to the French/Spanish or even Dutch faunal succession (Etouaires, Vialette, Villarroya, Roccaneyra, St. Vallier, Puebla del Valverde, Senèze, Tegelen) and also to Italian land mammal sites (Triversa, various sites in Lower and Upper Valdarno basins). Mein (1975, 1990) and Guérin (1980, 1982, 1990; Guerin & Faure, 1982) significantly contributed to the subdivision of the Villafranchian through the MN/MNQ zone-system. At the same time, the important works of Azzaroli and collaborators established a Villafranchian succession of Faunal Units (Azzaroli et al., 1982, 1988) that took its more or less final form in Gliozzi et al. (1997) (Fig. 2).

In the late years of the past century, a project coordinated by the University of Turin aimed to revise the stratigraphy of the "Villafranchian type area" (Carraro, 1996). However, the revision failed to understand the Villafranchian as a biochronologic unit and has been totally biased by the attempt to demonstrate the value of the Villafranchian as a continental stage (Caramiello et al., 1996).

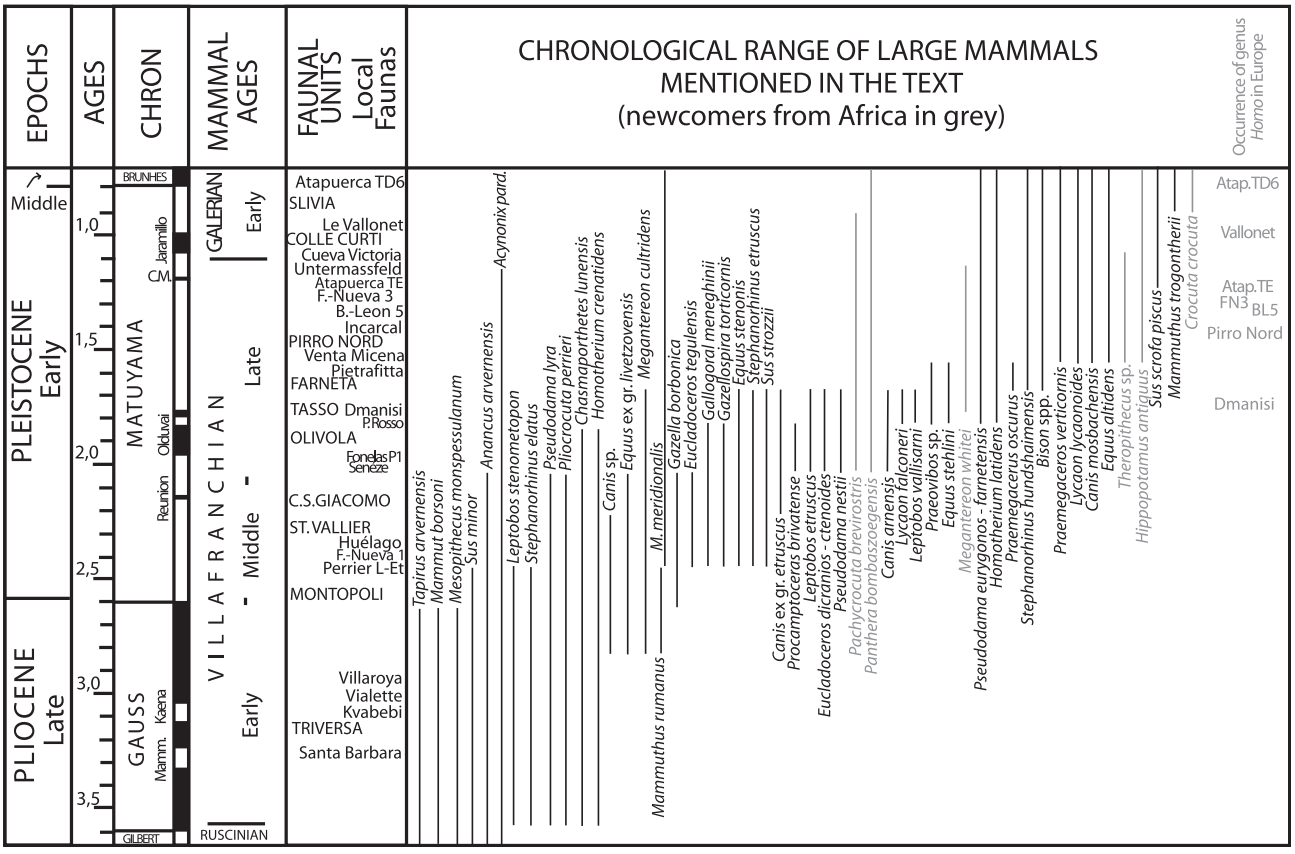

Fig. 2. The Villafranchian chronology with range chart of selected large mammals mentioned in the text. Newcomers from Africa in grey.

2. The Villafranchian Mammal Age: How this continental biochronologic unit is subdivided

2.1. Early Villafranchian

The large mammal fossil record in the Italian peninsula is very scarce for this part of the Pliocene, and the same is true for most of the European continent. The first significant late Pliocene record is given by the Early Villafranchian faunas of the Triversa Faunal Unit (FU) (Azzaroli, 1977; Azzaroli et al., 1988; Pradella and Rook, 2007). These mammalian assemblages still retain the subtropical affinities, which were typical of the previous Mammal Age (the Ruscinian). The Triversa faunal unit includes several taxa of humid forest affinities such as *Tapirus arvernensis*, *Mammut borsoni*, *Anancus arvernensis*, *Sus minor*, and *Mesopithechus monspessulanus*. These taxa are associated with new mammals, interpreted as more related to wooded environments, including *Leptobos stenometopon*, *Stephanorhinus elatus*, *Pseudodama lyra* among artiodactyls, as well as among carnivores the hyaenids *Pliocrocuta perrieri* and *Chasmaporthetes lunensis*, the sabertooth cat *Homotherium crenatidens*, and the large cheetah *Acinonyx pardinensis*.

Early Villafranchian faunas in Italy occur in Piedmont (Villafranca d'Asti basin) and along the western and southern side of Tuscany (e.g. Santa Barbara in Upper Valdarno basin). In France, the early Villafranchian is well recorded in the Central Massif at the site of Vialette where one of the first records of *Canis* and *Equus* are found in Europe (Lacombat et al., 2008) and in Spain it is registered at the site of Villarroya with one of the oldest records of *Meganteron cultridens* in the continent (Palmqvist et al., 2007). The Early Villafranchian is also characterized in Eastern Europe, at the Dacic Basin in Romania as well as in Bulgaria, by the appearance of a primitive form of the African origin modern elephant *Mammuthus rumanus* (Lister and van Essen, 2003; Markov and Spassov, 2003), the ancestor of *Mammuthus meridionalis*.

Other important sites across Europe and Asia (from Spain to Mongolia) are Huéscar-3 and Las Higueruelas (Spain), Les Etouaires (France), Tulucesti, Covrigi, Groserea and Cernatesti (Romania), Kvabebi (Georgia), Shamar (Mongolia) and Udunga (Transbaikalia) (Agustí et al., 2009; Mazo, 1989; Vislobokova et al., 1995, 2001; Oms et al., 1999; Radulescu and Samson, 2001; Lister and van Essen, 2003; Mazo et al., 2003; Lister et al., 2005) (Fig. 3).

Paleomagnetic study of the long sedimentary sequence of Santa Barbara quarry (Castelnuovo Synthem of the Upper Valdarno basin) discovered a long normal polarity interval interrupted at a few meters above the vertebrate-bearing level by a reversed polarity interval. The latter has been interpreted as the Kaena event within the Gauss Chron, on the basis of geological and paleobiological evidence (Torre et al., 1996; Napoleone et al., 2003; Ghinassi et al., 2004). On this basis, at about 3.2 Ma the faunal association regarded as typical of the early Villafranchian was already present in the Italian peninsula. The sedimentary succession of the Kvabebi site (Georgia) has also been recently calibrated by paleomagnetism (Agustí et al., 2009). The mammal community from Kvabebi is dominated by Eurasian taxa, although there are some African origin elements, i.e. *Kvabebihyrax kachethicus* (Vekua, 1972). A number of Holarctic origin elements from this site are shared with localities such as Triversa in Italy, Les Etouaires in France and, most specially, with Villarroya in Spain. According to the paleomagnetic signature of the Kvabebi sedimentary succession, this site should have an age close to 3.07 Ma (Agustí et al., 2009).

The beginning of the Early Villafranchian (i.e. the Ruscinian – early Villafranchian transition) and its position in the magnetochronological scale has been identified by various researchers within the earliest Gauss magnetochron (approximately between 3.6 and 3.5 Ma), thus falling (according to the recommendation approved by the International Union of Geological Sciences Executive Committee on June 29th, 2009) into Late Pliocene (Vangengeim et al., 2005).

2.2. Middle Villafranchian

The first Middle Villafranchian large mammal assemblage is Montopoli, in the Lower Valdarno basin (Tuscany). Montopoli is stratigraphically superposed on faunas of Triversa unit and to shallow-water marine sediments of Early Pleistocene age (Middle Pliocene in papers previous to the IUGS, 2009 decision; cf. Benvenuti et al., 1995). This fauna is celebrated in literature for its important signal of environmental change given by the dispersals of a primitive species of the genus *Mammuthus* (ascribed to *M. rumanus* by Lister and van Essen, 2003 but included within *M. meridionalis* by Palombo and Ferretti, 2005), the monodactyl horse (*Equus* cf. *livenzovensis*), the large deer *Eucladoceros tegulensis*, and *Gazella borbonica*, as well as the disappearance of some of the taxa with subtropical affinities still characterizing the previous Early Villafranchian assemblages (Pradella and Rook, 2007). The Montopoli Faunal Unit (corresponding to the MN16b unit in the European MN sub-division) was originally included in the Early Villafranchian (Azzaroli, 1977; Azzaroli et al., 1988), but the marked faunal turnover characterizing the transition from the Early Villafranchian Triversa FU to Montopoli FU suggested considering Montopoli as the basal unit of the Middle Villafranchian (Caloi and Palombo, 1996; Gliozzi et al., 1997). Montopoli and the related faunal unit occurs at the Gauss–Matuyama transition (Lindsay et al., 1980). Faunas of similar age, which contain archaic true horses and are correlative with the lowermost interval of reversed polarity in the Matuyama Chron, are known from several localities from former Soviet Union countries: Liventsovka (lower beds) and Khapry in Russia; Kryzhanovka (lower beds) in Ukraine; Kuruksai, Obigarm, Karamaidan, and Tutak in Tajikistan; southern Adyrgan in eastern Kazakhstan (Vangengeim et al., 2005) (Fig. 3).

The Early/Middle Villafranchian transition corresponds to the Gauss/Matuyama boundary (~2,5 Ma), thus correlating with the newly redefined Plio/Pleistocene boundary (Gelasian Stage, GSSP at Monte san Nicola Section, Sicily; Rio et al., 1994; Gradstein et al., 2004).

The Early to Middle Villafranchian turnover took place close to the Piacentian/Gelasian boundary and the so-called "elephant-*Equus* event" (Azzaroli, 1977; Lindsay et al., 1980) was driven by the "Glacial Plio/Pleistocene" climatic cooling, related to the onset of bipolar glaciations, as well by the effects of the transition to a climate characterized by glacial–interglacial fluctuations, influenced by the 41 ka orbital cycle of the obliquity variation (Shackleton, 1995). Despite the extensive use in literature, the term "elephant-*Equus* event" should be avoided for indicating the 2.5 Ma event, because both modern elephants (genus *Mammuthus*) and modern one-toed horses were already present in two Early Villafranchian sites of Europe: Dacic Basin (Radulescu and Samson, 2001; Lister et al., 2005), Vialette (Lacombat et al., 2008). At the Guadix-Baza Basin (Spain), the first occurrence of *Equus* was established in the uppermost part of the Gauss Chron or at the base of the Matuyama chron (Agustí and Oms, 2001).

The second Faunal Unit of the Middle Villafranchian (St. Vallier FU) is based on the fauna from the French site of Saint Vallier. The site and fauna have been recently exhaustively revised by an international research team (Guérin et al., 2004). Other important sites of Middle Villafranchian age are Varshets in Bulgaria and Sesklo, Dafnero, Vatera, Volakas in Greece (Spassov, 1997, 2000; Koufos, 2001; Kostopoulos and Athanassiou, 2005). Saint Vallier FU is followed by the Costa San Giacomo FU (Anagni Basin, Latium).

The faunal composition of middle Villafranchian units is characterized by some important first occurrences, including those of

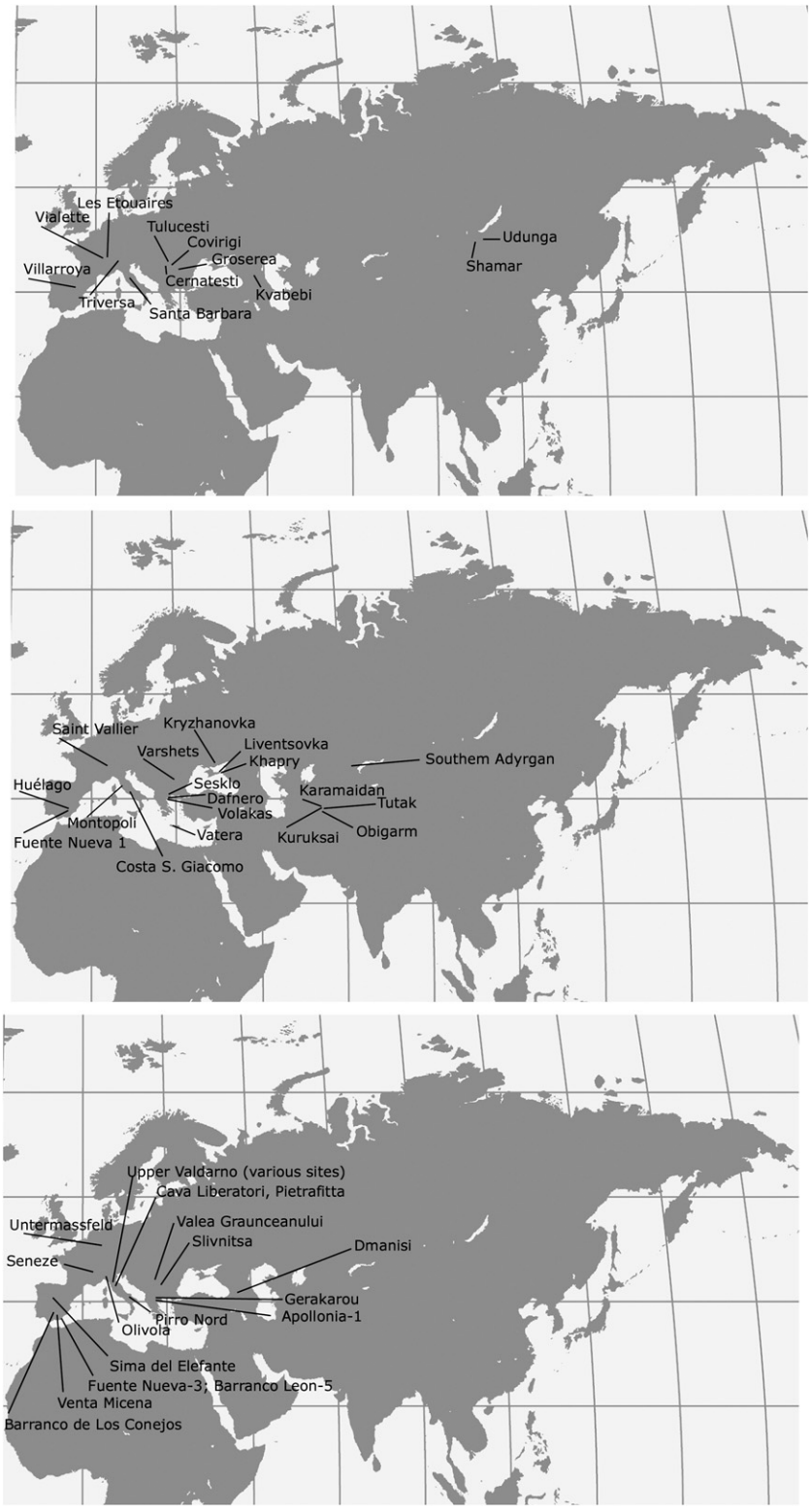

Fig. 3. Geographic distribution of Early (top), Middle (center), and Late (bottom) Villafranchian sites mentioned in the text.

Stephanorhinus etruscus, *Equus stenonis*, *Sus* cf. *strozzii*, the rupicaprine *Gallogoral meneghinii*, and the spiral horned antelope *Gazellospira torticornis*. Among carnivores, important is the first occurrence of *Canis* cf. *etruscus*, a taxon very common in the following units (Rook and Torre, 1996). The occurrence of *Canis* cf. *etruscus* in the Costa San Giacomo fauna, as was the finding of *Canis* sp. in the Early Villafranchian of Vialette, indicate how the so-called "Wolf-event" of Azzaroli (1983) started earlier than originally assumed, and that the expansion of wolf-like dogs across Eurasia was a diachronous event (Sotnikova and Rook, 2010).

2.3. Late Villafranchian

The late Villafranchian represents a time span longer than the previous sub-division of the Mammal Age. The faunal turnover that occurred just below and during the Olduvai normal subchron deeply affected mammal assemblages both in carnivore and herbivore faunal components. Most early Early Pleistocene (formerly "Pliocene") species disappeared, particularly among herbivores, and new carnivores and herbivores progressively appeared (Sala et al., 1992; Torre et al., 1992). The renewal from the middle to late Villafranchian is accomplished mainly by dispersal events, which succeeded in phases around the mid part of Early Pleistocene (or the former Pliocene-Pleistocene boundary when this was placed at Gelasian/Calabrian boundary, at 1.806 Ma; cf. Torre et al., 1992). In the original description of Azzaroli (1977), the late Villafranchian would include three Faunal Units: Olivola, Tasso and Farneta. Subsequently, a more recent fourth faunal unit (the Pirro Nord Fauna Unit), was added (Gliozzi et al., 1997).

The Olivola Faunal Unit is the first unit of the Late Villafranchian. It records a further change in faunal composition but also shows some continuity from the previous one of middle Villafranchian. In the Olivola Faunal Unit, the most widespread bovid is *Leptobos etruscus*. In the same unit also appear for the first time two derived forms of deer, *Eucladoceros dicranios–ctenoides* and *Pseudodama nestii* as well as the Caprinae *Procamptoceras brivatense*. Among the carnivores, is important the first appearance of the large hyaena *Pachycrocuta brevirostris* and of the fossil jaguar *Panthera gombaszoegensis*. While the Olivola local fauna is from northwest Tuscany (Lunigiana), local faunas of the Olivola FU (as well as faunas transitional to the following FU, the Tasso Faunal Unit), are also found in the Upper Valdarno Basin (Florence and Arezzo provinces) and represent the bulk of finds for the major part in historical collections A few recent discoveries (Mazza et al., 2004; Fig. 4) further document this Faunal Unit in Upper Valdarno. Important early Late Villafranchian large mammal associations occur also at Fonelas P-1, at the Guadix-Baza Basin in Spain (Arribas, 2008), Senèze in France (although the age of the site has been questioned in the past; Roger et al., 2000; Fig. 5), Valea Graunceanului in Romania, Slivnitsa in Bulgaria, and Gerakarou in Greece (Bolomey, 1965; Koufos, 1987, 2001; Koufos et al., 1992; Koufos and Kostopoulos, 1997; Malez et al., 1999) (Fig. 3).

Fig. 4. Excavation of Poggio Rosso bone accumulation in Upper Valdarno (Italy). Photo courtesy of F. Landucci.

Fig. 5. Excavation at the classical site of Senéze (France) in 2005. A skeleton of *Equus sthelini* photographed by S. Cooke. Photo courtesy of and copyright E. Delson.

Martínez-Navarro (2010) suggests naming this event as the "*Pachycrocuta brevirostris* event" because of the high impact of this giant supercarrion eater hyaenid in the Early Pleistocene faunal assemblages on the entire Eurasia geographic range, from the Iberian Peninsula to the eastern China and Indonesia. This species is the best recorded carnivore and the most important faunal accumulations agent in this continent during all the Late Villafranchain. This new term is more appropriate and is proposed to be substituted for the former "Wolf-event" as defined by Azzaroli (1983).

The transition from the Olivola to the subsequent Tasso FU has been magnetostratigraphically calibrated close to the top of the Olduvai Subchron (Napoleone et al., 2003). It thus correlates around the Gelasian/Calabrian boundary as defined at La Vrica (Aguirre and Pasini, 1985; Albianelli et al., 2002; Gradstein et al., 2004). This boundary is placed within an interval of gradual climatic transition which mirrors the gradual change in faunal composition.

The Tasso FU includes some new taxa, such as an ovibovine (*Praeovibos* sp; De Giuli and Masini, 1983, 1987), also recorded at the site of Barranco de Los Conejos in the Guadix-Baza basin, Spain (Agustí et al., 1987), the primitive wild dog *Lycaon falconeri* (Rook, 1994; Martínez-Navarro and Rook, 2003), the derived medium-sized deer *Pseudodama eurygonos–farnetensis* (Azzaroli, 1992), the small horse *Equus stehlini*, and the stout-built bovid *Leptobos vallisarni*. The antelopes *G. torticornis* and *P. brivatense* are no longer present. The Tasso FU also marks the last occurrence of several forms: the sabertoothed tiger *M. cultridens* (Martínez-Navarro and Palmqvist, 1995; Palmqvist et al., 2007), and the early wild dog *L. falconeri* (Martínez-Navarro and Rook, 2003).

Shortly after the Tasso FU, a new important faunal turnover is recorded in the Mediterranean Europe: the *Homo* dispersal. The earliest Hominins out of the African continent are recorded at the Caucasian site of Dmanisi in Georgia (Gabunia et al. 2000; Lordkipanidze et al., 2007), associated with the latest occurrence of *Canis etruscus* (Vekua, 1995; Sotnikova and Rook, 2010). In addition to Hominin occurrence, Dmanisi is the earliest site with

Fig. 6. The recovery of an elephant skeleton from the lignite mine of Pietrafitta (Umbria, Central Italy). Photo courtesy of S. Gentili.

Fig. 8. A group of *Pachycrocuta brevirostris* eating on a *Mammuthus meridionalis* carcass; life reconstruction based on evidences from the Orce sites (Guadix-Baza basin, Spain). Paleoart by Mauricio Antón.

new faunal elements colonizing Europe, some of them coming from Africa, such as the sabertoothed tiger *Megantereon whitei* (Martínez-Navarro and Palmqvist, 1995, 1996; Palmqvist et al., 2007), and others coming from Asia, such as the Caprini *Soergelia minor*, the spiral antelope *Pontoceros ambiguous*, or the buffalo *Bison georgicus* (Bukhsianidze, 2005; Lordkipanidze et al., 2007). Although Dmanisi records the first occurrence of *Pontoceros* and *Soergelia*, both genera seem to have invaded Southern Europe later.

In Italy, the faunal composition of the following Farneta FU (localities of Cava Liberatori in Val di Chiana and Pietrafitta in Upper Tiber valley) (Fig. 6) records two important new occurrences: the megalocerine group (with the species *Praemegaceros obscurus*; Abbazzi, 2004), and the rhinocerotid *Stephanorhinus* cf. *hundsheimensis* (Alberdi et al., 1998). At the same time a number of Villafranchian taxa have their last occurrence in this unit.

The Cava Pirro assemblage (Abbazzi et al., 1996) indicates a further episode of faunal renewal and represents the last faunal unit of the Late Villafranchian, the Pirro FU (De Giuli et al., 1987; Gliozzi et al., 1997). Important occurrences are: the middle size horse *Equus altidens*, the large deer *Praemegaceros verticornis*, the derived wild dog *Lycaon lycaonoides* (Martínez-Navarro and Rook, 2003), and the first occurrence in Europe of the large-sized African Geleda baboon *Theropithecus* sp. (Rook et al., 2004; Rook and Martínez-Navarro, in press.). The first occurrence of another

Fig. 7. Excavations at Venta Micenea, Guadix-Baza basin (Andalusia, Spain). a) General view on the three outcrops excavated during the 2005 season; b) detail on bone accumulation. Photo courtesy of J. Mestre.

Fig. 9. A sabertoothed tiger *Megantereon whitei* hunting a large deer *Praemegaceros verticornis*; life reconstruction based on evidence from the Orce sites (Orce, Guadix-Baza basin, Spain). Paleoart by Mauricio Antón.

Fig. 11. Untermassfeld research excavation 2008, polyspecific bone concentration in squares Q 30 and Q 31 with remains of *Bison menneri*, *Eucladoceros giulii*, *Stephanorhinus hundsheimensis* and *Mammuthus meridionalis*. Photo courtesy of Senckenberg Research Station of Quaternary Palaeontology, Weimar.

African taxon in this faunal unit (*Hippopotamus antiquus*) is recorded in the Spanish locality of Venta Micena (Figs. 7–9), in Orce, Guadix-Baza basin (Martínez-Navarro et al., 2004a). This mammal Faunal Unit is also well represented in Greece within the Mygdonia Basin, especially at the site of Apollonia-1 (Kostopoulos, 1997; Koufos and Kostopoulos, 1997; Fig. 10).

The oldest occurrence of early *Homo* in Western Europe is recorded in this faunal unit, documented by paleolithic artifacts associated with mammal remains. It is reported in southern Italy, at the site of Pirro Nord, in the *Allophaiomys ruffoi* "biozone" (Abbazzi et al., 1996; Arzarello et al., 2007), in southern Spain at the sites of Fuente Nueva-3 and Barranco Leon-5, in Orce, in the "biozone" of *Allophaiomys* aff. *A. lavocati*, a more evolved form than *A. ruffoi*, a synonym of *A. pliocaenicus* (Martínez-Navarro et al., 1997, 2004b; Oms et al., 2000; Agustí and Madurell, 2003) , and, more recently, also in southern France (Hérault; Crochet et al., 2009).

The latest Villafranchian in Europe is characterized by the arrival of the suid *Sus scrofa priscus*, and by the latest record of *M. whitei* in the continent, both recorded at the site of Untermassfeld (Fig. 11), Germany (Kahlke, 1997, 2001a, 2001b; Guérin and Faure, 1997; Hemmer, 2001; Palmqvist et al., 2007). A form of suid is also found at the lowermost levels of Sima del Elefante (Atapuerca, Spain), which is associated with human remains and lithic artifacts, dated around 1.2 Ma (Carbonell et al., 2008).

The Farneta and Pirro FUs record the Pleistocene part of the Late Villafranchian, an interval during which the faunas were gradually and still not completely displaced by the large mammals that characterize the following Galerian Mammal Age.

Extensive paleomagnetic investigations in the intermontane basins along the Apennine chain (Napoleone et al., 2003) have allowed the correlation of the late Villafranchian faunas to the geomagnetic polarity time scale. The Middle/Late Villafranchian transition thus is placed to occur within the reverse polarity Matuyama Chron in between the Reunion and Olduvai subchrons (Torre et al., 1992; Napoleone et al., 2003), which is around the GSSP of the Gelasian/Calabrian boundary (La Vrica Section; Aguirre and Pasini, 1985; Albianelli et al., 2002; Gradstein et al., 2004). The

Fig. 10. Excavations at Apollonia-1, Mygdonia basin (Macedonia, Greece). General view of the site. Photo courtesy of G. Koufos.

end of the Late Villafranchian (the Late Villafranchian–Galerian transition) also occurs within the Matuyama magnetochron, in between the K and Jaramillo subchrons around 1.1 Ma within the upper part of the Early Pleistocene (Napoleone et al., 2003).

3. The end of the Villafranchian and the beginning of the Galerian Mammal Age

The Colle Curti fauna (Central Apennine; Ficcarelli and Silvestrini, 1991; Abbazzi et al., 1998) represents the first faunal unit of the Galerian Mammal Age. This Faunal Unit is characterized by the latest occurrence in Europe of the giant hyaenid *P. brevirostris*, in sites including Vallonnet in France, or Cueva Victoria in Spain, and (slightly later) Slivia in Italy. Elements characteristic for this Faunal Unit are the dominant occurrence of *Hippopotamus*, of the megalocerine *P. verticornis*, and of *Bison (Bison)*. The Colle Curti and Vallonnet faunas have been assigned to the Jaramillo Subchron (Lumley et al., 1988; Moullé, 1992; Gagnepain, 1996; Torre et al., 1996; Coltorti et al., 1998).

The Colle Curti FU corresponds to the beginning of the most important faunal change of the Pleistocene. During this renewal, the Villafranchian taxa became extinct, or in some cases gave rise to new species more adapted to arid, cold climates. Here, the Galerian forms appear together with some of the direct ancestors of the 'modern' faunal elements through a sequence of dispersal events (Azzaroli, 1983).

Colle Curti (and the subsequent Slivia FU; Ambrosetti et al., 1979; Gliozzi et al., 1997) occurs within the interval that apparently corresponds to the long transition between climates forced by the 41 ka cycles and the later 'glacial' climate characterized by the alternation of pronounced glacial–interglacial periods modulated by the 100 ka periodicity (Shackleton, 1995). The transition from Villafranchian to Galerian Mammal Ages approximates the latest part of the Early Pleistocene. Since the latter is a time span (about from 1.2 to 0.6 Ma) characterized by deep and crucial changes in the global climate system, the transition from Villafranchian to Galeran Mammal Ages represents a major episode in mammalian fauna reorganization and would deserve a wider re-evaluation. The mammalian faunal community of this time span localities primarily includes survivors from the latest Villafranchian, as well as more evolved forms characteristic of the beginning Middle Pleistocene. Due to the lack of a term commonly used for larger mammal associations of the Late Villafranchian/early Middle Pleistocene transitional zone in Eurasia, two different names have been proposed: Epivillafranchian (Kahlke, 2000, 2007), and Protogalerian (Caloi and Palombo, 1996; Palombo, 2004). Although not formalized yet, the former seems to have been more widely introduced in the literature (e.g. Nikiforova, 1987; Alba et al., 2008; García et al., 2008).

4. Final remarks

Environmental and climatic change are forcing factors for mammal dispersal events and evolutionary changes. Both phenomena are the bases of defining biochronology scales. Much more common than evolutionary changes in Plio-Pleistocene large mammal history are dispersal events. The latter are by definition diachronic events (in some cases also at regional scale, when we limit our observation to Western Europe), and this has, as a consequence, two important aspects for a proper understanding of large mammal biochronology: i) The decrease in accuracy of biochronological framework on large scale correlation. High rank biochronological units (the Land Mammal Ages), based on events which have a regional or continental significance are useful tools for chronological correlations, while lower rank bichronological units (Faunal Units) have a more restricted, regional correlative significance; ii) Biochronologic schemes and units are to be considered working tools, suitable of update and flexible to be changed/revised according to the ongoing knowledge of mammal communities evolution and their fossil record.

Since the original definition by Pareto (1865) and the assessment of Villafranchian sub-division by Azzaroli and colleagues (Azzaroli, 1970, 1977; Azzaroli et al., 1988; Gliozzi et al., 1997) the Villafranchian biochronological sub-division (Mammal Ages and Faunal Units), has been mainly based on mammal faunas from different sedimentary basins and fossiliferous sites in Italy and France. Although continuous local records are important in the resolution of faunal changes through time, the impact of such an approach in the definition of large scale biochronological units (as Villafranchian it is) is certainly limited since it is biased by regionalism and misses diachronicity of events. The definition of Villafranchian is traditionally stocked in the Italian/French record (thus at regional scale), but noticeable improvement in understanding of the biological history of this time span comes from including into the biochronologic frame a number of sites that in the recent decades have yielded crucial information, from Spain to Greece and western former Soviet Union countries.

A better understanding of faunal evolution and turnover events is emerging when is possible to follow up these changes within the same sedimentary basin in a continuous well calibrated correlatable stratigraphic succession. A number of southern European basins have been exploited in recent years:

1) In Spain the Guadix-Baza basin (Granada, southern Spain), where a long continuous continental sedimentary succession encompass the entire time span representing the latest Miocene, the Pliocene and most of the Pleistocene, with a very good record of Early, Middle and Late Villafranchian mammal faunas (Moyà-Solà et al., 1987; Alberdi and Bonadonna, 1989; Martínez-Navarro, 1991; Agustí et al., 2001; Toro et al., 2003; Arribas, 2008).
2) in Bulgaria and Greece, a suite of sites are providing important information especially on crucial time span as the Middle and early Late Villafranchian (Koufos and Kostopoulos, 1997; Spassov, 1997, 2000, 2003; Koufos, 2001).
3) In Georgia, south of the Caucasus, where the fossil record of large mammals ranges from the Late Pliocene to Early Pleistocene (Agustí et al., 2009; Vekua, 1986, 1995; Lordkipanidze et al., 2007).

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