

## REMARKS ON THE BIOCHRONOLOGY OF MAMMALIAN FAUNAL COMPLEXES FROM THE PLIOCENE TO THE MIDDLE PLEISTOCENE IN FRANCE

Maria Rita Palombo\*<sup>°</sup>, Andrea Maria Francesco Valli\*<sup>•</sup>

\* *Dipartimento di Scienze della Terra, Università "La Sapienza, Piazzale A. Moro, 5 - 00185 Roma, Italy*  
*e-mail: mariarita.palombo@uniroma1.it*

<sup>°</sup> *CNR- Istituto di Geologia Ambientale e Geoingegneria - Roma, Italy*

<sup>•</sup> *Istituto Italiano di Paleontologia Umana, Piazza Mincio 2 - 00100 Roma, Italy*

**ABSTRACT** - Some French large mammal assemblages, from the Pliocene to the Middle Pleistocene, have been critically valued in the aim to operationally define biochronological unit characterised by taxonomical and ecological homogeneity. Following the previous biostratigraphical schemes thus far proposed, for each biochron (represented by a complex of local faunas, characterised by first/last appearances bioevents, evolutive degree of the taxa belonging to well defined phyletic lines, co-occurrence of well-defined large mammal taxa) "MN" and "MNQ" denomination has been maintained.

The most important bioevents and faunal renewals can be correlated with significant Early and Middle Pliocene (MN14-MN16a), forest dwelling taxa clearly prevailed, nonetheless some taxa inhabiting open environmental progressively increased. During the following Pliocene and at the beginning of the (MN16b-MNQ19), the percentage of taxa inhabiting grassland or temperate warm savanna augmented, whereas at the end of the Early and at the transition with the Middle Pleistocene (MNQ20) taxa suggesting more arid climatic conditions prevailed, During the following Middle Pleistocene (MNQ22-24), taxa typical of cool or cold grassland (reindeer, mammoth, woolly rinocherous) widespread until Mediterranean coast. During the Late Pleistocene the French fauna progressively acquired a modern configuration.

In appendix some local faunas are presented following the biochronological scheme here proposed.

**KEY WORDS:** Large mammal faunas, Plio-Pleistocene, France, Biochronology.

### FOREWORDS

The field of biostratigraphy and biochronology (terms that cannot be considered as synonymous), applied to continental mammal faunas, has a great deal of problems. The most important consists in the different operational and theoretical approaches followed by the different scientists (Walsh, 1998, and references therein). In fact, in a continental environment, due to taphonomic and sampling biases, fossil remains of taxa characterising a given biochronological unit do not necessarily appear in each section. Furthermore, the stratigraphic order of their lowest/highest known occurrences does not necessarily reflect the temporal order of their first/last appearances within a specific local subarea.

Consequently, the boundaries of the large mammal biochrons can be defined only theoretically by using palaeobiological events (e.g. the appearance/origination and disappearance/extinction of one or more taxa), and not operationally by using the stratigraphic data following biostratigraphic principles, even if such data correspond to the oldest/latest known fossil record (Walsh, 1998, and references therein). Therefore, the boundaries of a biochronological unit cannot be defined only on the basis of the earliest "historical appearance" or effective extinction of one or more taxa, bioevents that occurred in a not well defined span of time before their lowest or after their highest occurrences in the fossil record.

Consequently, the lowest/highest occurrences of a taxon within a given section should not necessarily define the actual beginning/end of the biochron to which the taxa belong. Accordingly, the term "biozone" seems

unsuitable to define biochrons in the case of continental large mammal faunas. We assume that a biochronological unit can be operationally represented by complex of local faunas, characterised by the co-occurrence of well defined large mammal taxa, or first/last appearances and, consequently by their taxonomical and ecological homogeneity for which the actual temporal extension cannot be defined.

The European biochronological schemes thus far proposed found principally on definition of faunal units (FUs, mainly used by Italian palaeontologists) and Mammal Ages (MAs) and "biozones".

The FU, based on all species from local faunas selected as a typical association (see Azzaroli, 1977; 1982; Gliozzi et al., 1997; Palombo et al., 2003), represents the biochron of the lowest rank. The FUs can be grouped in higher-level faunal complexes as the MAs.

Biochronological schemes based on "biozones" have proposed by Mein (1975) for the Mammal Neogene Units (MN) and by Guérin (1982) for the Pleistocene "Mammifères Néogènes et Quaternaires Biozones" (MNQ). After Mein (1998, and references therein) and Guérin (1982) each "biozone" is defined by: 1) the first appearance (either origination or immigration) of new taxa, 2) the evolutionary stage reached by selected, well-defined lineages of mammals and 3) the presence of peculiar taxa associations. The MN system is mainly based on occurrences of micromammals (especially rodents), whereas Guérin defined his biochrons by using mainly, but not exclusively, large mammals (Guérin, 1982,1990; Guérin & Patou-Mathis, 1996). Guérin

(1982, 1990) established new biochrons from the end of the Pliocene up to the beginning of the Holocene. He called them MNQ (Mammifères Néogènes and Quaternaires) and numerated them from 18 (late Villafranchian) up to 26.

MN and MNQ “biozones” have constituted the basis for the French biochronological framework. Anyway, several French authors (e.g. Bonifay, 1990; Mein, 1975, 1990, 1998; Guérin, 1982, 1990; Guérin & Patou-Mathis, 1996; Heintz, 1970; Chaline, 1997; Legendre & Lévêque, 1997) played attention to biochronological problems and some of them elaborated biochronological schemes for the Western Europe mammal faunas. For example, Heintz (1970) considered the Villafranchian (see Pareto, 1865, Carraro, 1996) as a biochron including the Middle and Late Pliocene. The French scientist divided his Villafranchian in four biochrons, early, middle, late and latest Villafranchian on the basis of taxa belonging to phyletic lines of cervid taxa (phyletic lineages of *Eucladoceros*, *Croizetoceros* and “*Pseudodama*”, sensu Azzaroli, 1992).

At the present time, the European Mammal Neogene System (NM) is the most followed biochronological tool for the Western Europe Neogene biochronology, also thanks to the contributions of many other authors from different countries (see, e.g. Bruijn et al., 1992; Agustí et al., 2001). The MN units have been recently calibrated on the basis of the magneto/biostratigraphic framework developed for some Spanish basins (Agustí et al., 2001; van Dam, 2001).

Although the theoretical approach of the French authors, which based their subdivision on the “biozone”, is slightly different from that of Italian ones that use the “faunal unit”, practically all the biostratigraphical/biochronological systems are used in the same way. Indeed, each biochron (“biozone” or faunal unit) corresponds a complex of taxa, mainly species or subspecies, that differ from the previous and the following complexes by the first appearance (to identify FUs also the last appearance has been took into consideration) of some taxa or by the evolutive degree of the taxa belonging to well defined phyletic lines.

On this basis, some French large mammal assemblages (appendix) from the Pliocene to the Middle Pleistocene have been critically valued taking into account the biochronological schemes proposed up to date for the Italian large mammal faunas (Gliozzi et al., 1997; Petronio and Sardella, 1999; Palombo in press; Palombo et al., in press and references therein) (Fig. 1).

**DISCUSSION**

Pliocene large mammal faunas are known since the beginning of XIX century from several localities in France. Moreover, several Pliocene taxa have been erected for specimens belonging to French faunas (see inter alios Bravard, 1828; Croizet & Jobert, 1828; Pomel, 1846; Depéret & Mayet, 1911; Viret, 1954). The

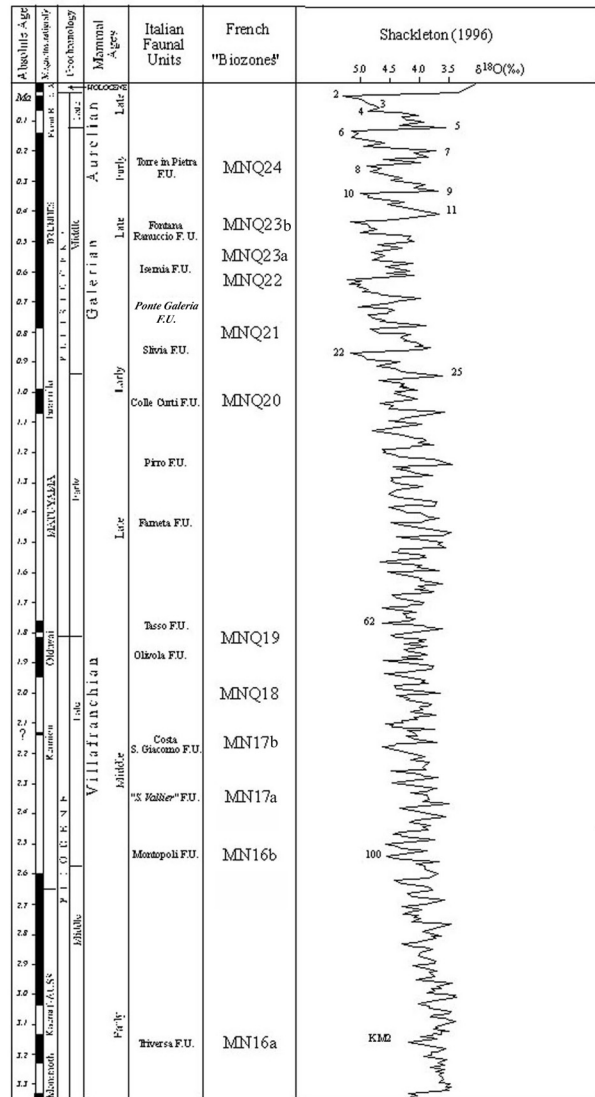


Fig. 1 - Biochronological scheme of large mammal faunal complexes of Italian peninsula and France from the Pliocene to the Middle Pleistocene.

richness of the Pliocene fossil record combined with the scarcity of the latest Miocene faunas (MN13) emphasises the turnover from the Turolian to the Ruscinian MAs (Tab. 1).

Indeed, a faunal renewal involving all the *ordina* characterised the beginning of the Ruscinian MA (MN14-15): aside some lineages persisting from the Miocene (*Hipparion* and *Hyracoidea*) new taxa made their first appearance in France. Among the carnivores the following genera appeared: *Meles*, with *M. genevauxi*, *Ursus*, with *U. minimus*, *Agriotherium*, with *A. insigne* (Argant & Crégut-Bonnoure, 1996; Aguilar et al., 1997). The first two were typical woodland-dweller species.

However, the taxa which first occurred at this time also concerned Proboscidea, Perrissodactyla and Artiodactyla. *Anancus arvernensis* first appeared in France (Guérin, 1996a), as well as *Dicerorhinus megarhinus* and *Tapirus arvernensis*, *Parabos cordieri* and *Korhynchoerus provincialis*. “*Cervus*” *pyrenaicus* is also assumed to first appear during the early Ruscinian.

This species, named "*Croizetoceros*" *pyrenaicus* by Azanza (2000) and Azanza et al. (1997) could have been present since the Latest Miocene (MN13). Instead, diversity of hipparionine horses decreased (Agustí & Antón, 2002) even if *H. crassum* was present in several Ruscinian localities.

During the early Ruscinian (MN14) the faunal complexes forest-dwelling taxa that preferred warm and humid climatic conditions, still prevailed, as it is confirmed by the presence of taxa such as *T. arvernensis*, *D. megarhinus* and small size cervid species belonging to the Muntiacini as well as by the palinological data (Fauquette et al., 1998, 1999). Instead, the presence of the genus *Gazella* is representative of open landscapes.

The transition to MN15 is characterised by the appearance of some Canidae (*Nyctereutes donnezani*, *Eucyon adoxus*), and of *Lynx issiodorensis*, a long persistent taxa that will also survival during the Villafranchian, as well as of *Pachycrocuta pyrenaica*, a scavenger which probably dwelled in open lands as all the extant taxa belonging to Hyaenidae. Among the herbivores new species joined the guild of forest-dwellers: two pachyderms, *Stephanorhinus miguelcrusafonti* and *Mammuth (Zygodolophodon) borsoni* as well as the first representative of the genus *Sus*, *Sus minor* (= *S. arvernensis*). The cat *Felis christoldi* was taken over by *F. aff. F. maniculata* and the large bovid *Parabos cordieri* by *Alephis liryx* (notice that this species might have occurred since the early Ruscinian in Italy; Bianucci et al., 2001). A significant renewal of the small cervid taxa was also recorded. The Hyracoidea were definitively extinct, whereas *Orycteropus depereti*, a survival from the Miocene fauna (Agustí & Antón, 2002), was found in the Perpignan fauna (MN15). The whole of the fauna was still consistent with the prevalence of closed woodlands, but the persistence of *Gazella* and the appearance of *Pachycrocuta* suggest the presence of some open landscape.

Since the early Villafranchian (MN16a, corresponding to Italian Triversa FU) the typical open-land mammals began improving their number, in accordance with first pulse of the Pliocene glacial trends, taking place around 3.2/3.1 Ma. In France, taxa such as *Acinonyx pardinensis*, *Chasmaporthetes lunensis*, *Pachycrocuta perrieri* (which evolved from *P. pyrenaica*; Howell & Petter, 1980) together with *Megantereon cultridens* first appeared. *Gazella* was present with *G. borbonica* and two species of genus *Leptobos*, *L. bravardi* and *L. elatus* were first reported (Duvernois, 1990). Both genera are considered as inhabiting open-lands. As far as cervids are concerned, the renewal was marked by the appearance of large deer, *Arvernoceros ardei* and "*Cervus*" *perrieri*, and of the middle-sized "*P.*" *pardinensis* belonging to lineage of French "*Pseudodama*" (see Appendix for a discussion).

Among the Rhinocerotidae, the genus *Dicerorhinus* was taken over by *Stephanorhinus*, with the long survival species *S. etruscus*.

The beginning of the middle Villafranchian (MN16b, corresponding to the Montopoli FU) took place approxi-

mately during the global climatic change happened at about 2.7-2.5 Ma ago. The dispersion bioevent, also known as the "elephant and *Equus* event" (Lindsay et al., 1980; Azzaroli, 1983; Azzaroli et al., 1988) is testified in France by the appearance of *E. stenonis* in the Roccaneyra local fauna, together with *Hipparion rocinantiss* that marks its lowest occurrences in Western Europe (Guérin, 1996b). Moreover, new open land dwellers, *Gazellospira torticornis* and *?Procamptoceros brivatense*, first appeared; among large deer, *Eucladoceros* occurred whereas *A. ardei* and "*C.*" *perrieri* have not recorded yet.

The first appearance bioevents of *Ursus etruscus*, *Viretailurus schaubi* and *Gallogoral meneghini* as well as the local evolution of cervids mark the transition to the following biochron (MN17a, circa corresponding to Italian "Saint Vallier" or Colle Pardo FU). During this time the large mammal faunas showed a further increasing in the taxa, which indicate the open environment.

Nevertheless, the presence of woodland-dwellers in some local faunas (e.g. Saint-Vallier, Drôme; Heintz, 1970; Valli, 2001) proves the existence of forest environments.

Inside assemblages ascribed to MN 17, a faunal complex (biochron MN17b, probably corresponding to Italian Costa San Giacomo FU) different from the previous MN17a, (typically represented by Saint-Vallier local fauna) can be distinguished basing on the following data derived from Chilhac LFA (Bœuf, 1990): (i) the advanced features of *A. arvernensis chilhiacensis*; (ii) the peculiar features of *E. stenonis guthi*. A large Canidae (already considered as further evidence, together with the Costa San Giacomo (Biddittu et al., 1979), of the Late Pliocene widespread of *Canis* similar to *Canis etruscus* in Europe) is known at Chilhac (Monguillon-Douillet, 2000) but its systematic position is not clear yet. On the basis of some absolute K/Ar and palaeomagnetic data, an age older than 1.9 Ma, could be retained for the Chilhac LFA (Bœuf, 1997).

The faunal assemblages thus far attributed to MNQ18 seem to be "transitional" from the middle and late Villafranchian faunal complexes as defined for the Italian peninsula (cfr. Gliozzi et al. 1997; Torre et al. 2001; Palombo, in press). In fact, the MNQ18 faunas, particularly the debated local fauna assemblage from Senèze (see Faure et al., 2002 and references therein), were characterised on the hand by the persistence of early-middle Villafranchian taxa, such as *Nyctereutes*, on the other by the disappearance of some other middle Villafranchian taxa, such as *Anancus* and *Gazella* disappeared (for a discussion on *Gazella* see Heintz, 1971) and by lowest occurrence of *Megolovis latifrons* (Crégut, 2002). Other taxonomic novelty is the presence of a *Felis* species, *F. silvestris lunensis*, also known at the latest Pliocene Italian site of Poggio Rosso (Mazza et al., in press), for which a latest Pliocene age can be inferred (Mazzini et al., 2000; Napoleone et al., 2003; Mazza et al., in press).

Moreover, in Senèze assemblage, the genus *Canis* is present with a form called *Canis* aff. *C. arnensis* by

Taxa	Ruscinian		Villafranchian						Galerian			Aurelian
	MN14	MN15	early	middle		?	late	early	middle	late	early	
			MN16a	MN16b	MN17a	MN17b	MNQ18	MNQ19	MNQ20	MNQ22	MNQ23a	MNQ23b
<b>PRIMATES</b>												
<i>Macaca sylvanus sylvanus</i>												
<i>Macaca sylvanus florentinus</i>												
<i>Macaca sylvanus priscus</i>												
<i>Paradolichopetecus</i> sp.												
<i>Paradolichopetecus arvernensis</i>												
<i>Mesopithecus monspessulanus</i>												
<i>Doilichopithecus ruscinensis</i>												
<b>CARNIVORA</b>												
<i>Nyctereutes donnezani</i>												
<i>Nyctereutes megamastoides</i>												
<i>Vulpes alopecoides</i>			?									
<i>Vulpes vulpes</i>												
<i>Vulpes praeglacialis</i>												
<i>Alopex lagopus</i>												
<i>Canis</i> aff. <i>C. armenesis</i> / <i>C. mosbachensis</i>												
<i>Canis senesensis</i>												
<i>Canis</i> aff. <i>C. etruscus</i>												
<i>Canis lunellensis</i>												
<i>Canis lupus</i>												
" <i>Canis</i> " sp. 1												
" <i>Canis</i> " <i>Michauxi</i>												
<i>Eucyon adoxus</i>												
<i>Cuon stehlini</i>												
<i>Cuon priscus</i>												
<i>Baranogale antica</i>												
<i>Enhydriactis ardea</i>												
<i>Aonyx bavardi</i>												
<i>Lutra affinis</i>												
<i>Lutra</i> sp.												
<i>Plesiogulo monspessulanus</i>												
<i>Gulo gulo</i>												
<i>Meles genevauxi</i>												
<i>Meles thoralis</i>												
<i>Meles meles</i>												
<i>Martes</i> sp.												
<i>Mustela palerminea</i>												
<i>Mustela praeivalis</i>												
<i>Mustela erminea</i>												
<i>Mustela nivalis</i>												
<i>Mustela putorius</i>												
<i>Mustela eversmanni</i>												
<i>Viverra zibethica</i>												
<i>Agriotherium insigne</i>												
<i>Ursus minimus</i>												
<i>Ursus etruscus</i>												
<i>Ursus deningeri</i>												
<i>Ursus spelaeus</i>												
<i>Ursus arctos</i>												
<i>Ursus thibetanus</i>												
Hyaenidae indet.												
<i>Hyaena prisca</i>												
<i>Pachycrocuta pyrenaica</i>												
<i>Pachycrocuta perrieri</i>												
<i>Pachycrocuta brevirostris</i>												
<i>Crocuta crocuta</i>												
<i>Chasmaporthetes lunensis</i>												
<i>Felis christoli</i>												
<i>Felis</i> aff. <i>F. maniculata</i>												
<i>Felis sylvestrina lunensis</i>												
<i>Felis sylvestrina sylvestrina</i>												
<i>Lynx issiodorensis</i>												
<i>Lynx pardina spelaea</i>												
<i>Viretailurus schaubi</i>												
<i>Panthera</i> ex gr. <i>P. gombaszoegensis</i>												
<i>Panthera leo fossilis</i>												
<i>Panthera leo spelaea</i>												
<i>Panthera pardus</i>												
<i>Acinonyx pardensis</i>												
<i>Dinofelis diastemata</i>												
<i>Homotherium crenatidens</i>												
<i>Homotherium</i> aff. <i>crenatidens</i>												
<i>Homotherium</i> ex gr. <i>H. latidens</i>												
<i>Megantereon cultridens</i>												
<b>PROBOSCIDEA</b>												
<i>Mammuth (Zygodon) borsoni</i>												
<i>Anancus arvernensis</i>												
<i>Anancus arvernensis chilensis</i>												
<i>Mammuthus meridionalis</i>												
<i>Mammuthus primigenius</i>												
<i>Elephas (Palaeoxodon) antiquus</i>												

Tab. 1 - Table of distribution of the French taxa from the Pliocene to the Middle Pleistocene. (continued)

Schaub (1943) and successively renamed *C. senesensis* by Martin (1973). Nonetheless it worth noticing that, according to some researchers' opinion, more than one fossiliferous level crop out at Senèze (see Azzaroli et al., 1997, but also Bonifay, 1992, for the opposite thesis).

After Azzaroli et al. (1988 and references therein), at

Senèze two different faunas would be present, respectively older and younger than those ascribed to Olivola FU; whereas Torre et al. (1992) erected the new Senèze FU (already recognised as the referential fauna for the MNQ18; Guérin, 1982), considering this faunal complex as showing an intermediate evolutive degree between





Saint Vallier and Olivola FUs. In effect, the taxonomical composition of the Senèze fauna/s differs from the faunal complexes of Costa San Giacomo and Olivola essentially because of the lack of *Anancus* and *Gazella* as well as *Pachycrocuta brevirostris* and *Panthera gombaszoegensis* respectively. The ongoing investigation performed by Faure, Guérin and Delson will clarify the actual composition of Senèze local fauna/s, the possible diachronicity between Italian and France highest occurrence of *Anancus*, and the lowest occurrence of *Pachycrocuta brevirostris*, *Panthera* and of “*Canis arnensis*” lineage.

A late Villafranchian cachet characterised the taxonomical composition of the faunal assemblages ascribed to the following MNQ19 biochron (possibly corresponding to Olivola-Tasso Italian FUs) characterised by an important faunal renewal, mainly depending of the local extinction of several taxa. Among the carnivores *Nyctereutes* and *Megantereon* disappeared, and *L. issiodorensis* was taken over by *L. pardina spelaea*. Among the herbivores *Croizetoceros ramosus*, *Gazellospira*, *Procamptoceros*, *Gallogoral* and *Pliotragus* were no more recorded, while the genus *Leptobos* was represented only by the species *L. etruscus*. On the other hand, the open-dweller *Pachycrocuta brevirostris* lowest occurred (La Sartanette, Gard), and in the cervid guild the more advanced “*Pseudodama*” *rhenanus perolensis* and *E. tetraceros* substituted “*P.*” *rhenanus philisi* and *Ecladoceros ctenoides senezensis* respectively.

It is worth noting that the late Villafranchian faunas seem less preserved in France than in Italy: only few fossiliferous localities can be ascribed to MNQ18 and MNQ19. Difficulties in correlating the French faunas with the classic late Villafranchian associations from Valdarno might be due to biases in the fossil record. E.g. typical late Villafranchian species such as *Lycaon falconeri* (Martinez Navarro and Rook, 2003) seems not recorded in France, whereas *Panthera* ex gr. *P. gombaszoegensis* lowest occurred only in the local faunas already ascribed to the following biochron MNQ20. The faunal list of LFAs ascribed to MNQ 20 as well as that of the late Early Pleistocene Italian faunas (Jaramillo submagnetozone, early Galerian, sensu Gliozzi et al., 1997) already known as “transitional faunas” (Bonifay, 1978; Azzaroli et al., 1988 and references therein), also includes “Galerian” taxa.

The renewal characterising the MN20 biochron depends on the disappearance of several Villafranchian taxa taken over by species that will persist during the early Middle Pleistocene. The mammal making their lowest occurrence in France are, among carnivores, *Ursus deningeri* (by opposite *U. etruscus* became extinct at this time) *Panthera* aff. *P. pardus* (the lowest occurrence in Europe is at Le Vallonnet site; Turner & Antón, 1997) and *P.* ex gr. *P. gombaszoegensis*, *Canis* ex gr. *C. arnensis*/*C. mosbachensis*, while among herbivores *Equus suessenbornensis* and *E. altidens* appeared (while *E. bressanus* and *E. stenonis* are no more recorded) and

*Stephanorhinus hundsheimensis* replaced *S. etruscus*, In addition, the Villafranchian cervid vanished and there are taken over by taxa such as *Capreolus capreolus suessenbornensis* and by the genus “*Praemegaceros*”. the lineage of the moose survived with *Cervalces carnutorum*, which was replaced by the late Villafranchian species *C. gallicus*. Also *Leptobos* disappeared, whereas some new bovids occurred, such as *Bison schoetensacki*, *Soergelia brigittae* and the genus *Hemitragus* as well as *Hippopotamus*, which made its lowest occurrence in France (Seinzelles and Soleilhac, Haute Loire) at the beginning of the Middle Pleistocene (Guérin, 1996c). *Mammuthus meridionalis* was still present with specimens characterised by advanced features, whereas *Elephas (Palaeoxodon) antiquus* was first reported from Soleilhac (Haute Loire), a site calibrated with the Jaramillo submagnetozone (Thouveny & Bonifay, 1984). During the MNQ 20 biochron (possibly corresponding to the Italian Colle Curti/Slivia FUs), taxa typical of open habitats (horses, *Mammuthus* and *Hemitragus*) were more common than those inhabiting woodlands (like panther, roe deer).

A new faunal renewal took place during the following early Middle Pleistocene as documented by the faunal associations so far ascribed by Authors to MNQ21 (very rare in France), to MNQ22 and MNQ23 *partim*; these two later (MNQ22 and MNQ23a) might be correlated with the Italian Isernia FU.

During MNQ 22, among the carnivores, *Vulpes vulpes*, *Gulo gulo*, *Panthera leo fossilis*, as well as *Ursus thibetanus* and *Hyaena prisca* first appeared. Among the herbivores, a new species of rhinoceros, *Stephanorhinus kirchbergensis*, was present, *Cervus elaphus* was characterised by archaic morphotypes, and *Hemitragus bonali* took over the more primitive *H. orientalis*. During this biochron the highest occurrence of *Homotherium* in France was recorded, whereas the genera “*Pseudodama*”, *Soergelia*, and *Cervalces* vanished.

During the following biochron (MNQ23a) the renewal was completed by the appearance of some other carnivores (*Canis* “*lunellensis*”, which some people put on the wolf lineage (Bonifay, 1971), *Cuon prisca*, *Crocuta crocuta*, *Ursus arctos*), of a third species of *Stephanorhinus*, *S. hemitoechus*, while the horses were represented by caballin *Equus* and by *Equus hydruntinus*, which will survive until the Holocene. *Dama clactoniana* and *Rangifer tarandus* are both present in France during this period, as well as *Bos primigenius*.

In the following biochron (MNQ23b, roughly corresponding to Fontana Ranuccio Italian FU), the renewal interested both carnivore and herbivore guild, but in some case at subspecific level: the larger *Panthera leo spelaea* substituted *P. leo fossilis*, the modern roe deer *C. capreolus capreolus* took over the more archaic subspecies. Moreover the lowest occurrence in France of genus *Rupicapra*, *Praeovibus prisca*, and *Bison prisca* has been reported. However, the lineage of “*Praemegaceros*” was dubitatively reported.

Finally, the transition to the last Middle Pleistocene

biochron (MNQ24; approximately corresponding to Torre in Pietra Italian FU) is highlighted by the first appearance of some typical "prehistoric" taxa like *Mammuthus primigenius* and *Megaloceros giganteus*.

Also *Coelodonta antiquitatis* appears, while *S. hundsheimensis* vanished. Nevertheless, up to three species of rhinoceros, *S. kirchbergensis*, *S. hemitoechus*, and *C. antiquitatis* can be found contemporaneously at the same site (La Fage, Corrèze, Guérin, 1973). Among the carnivore *Canis lupus* (lowest occurring in local faunas correlated with OIS 9, e.g. Caune de L'Arago, complex supérieur, Moigne et al., in press) and the modern mustelid of the genus *Mustela* appeared. *Vulpes praeglacialis* was taken over by *Alopex*, and *Ursus deningeri* by *U. spelaeus*, the cave bear. Among the herbivores, *H. cedrensis* took over of *H. bonalis*. During the Late Pleistocene the French fauna progressively acquired a modern configuration which will be reached with the megafauna extinction at the end of the Pleistocene, when *Mammuthus*, *Coelodonta*, *Ursus spelaeus*, *Megaloceros* disappeared.

### CONCLUSION

Since the Pliocene the France mammal faunas show the progressive increasing of elements that indicate a reducing of the vegetation cover (woodlands and forest). However such a change did not happen suddenly but it was quite progressive; in fact the early Pliocene faunas still show a predominance of forest-dwelling taxa.

Around 3.2 Ma a cooling phase took place, in which the climate became cooler and drier as documented both in marine and in continental environments (Shackleton 1995). The renewal of mammal assemblages is a global event, evident in the fossil record of Europe as a whole.

The French faunal complex of the MN16a, though renewed with respect to Ruscinian faunas, maintain moist forest characters, as indicated by the presence of the highest number of forest taxa and arboreal omnivores.

The climate worsening occurred around the Gauss/Matuyama boundary (oxygen isotopic stage (OIS) 104, Shackleton 1995; Partridge 1997; and reference therein) coincided with a profound change in the European flora and fauna. This major biotic event, is also evident in French MN16b faunal assemblages, characterised by a marked dwelling of forest taxa, while sever-

al new herbivores, large-sized mammals and pachyderms appeared. After the Middle Pliocene climate worsening, in the time span included between the Reunion normal magnetic episode and the Olduvai magnetochronozone (MN17a, b biochrons) a slight lowering of the temperature altered the vegetation, at least in the Western Mediterranean area, giving rise to more open environments (Suc et al. 1995). Among other bioevents, during this time a further faunal renewal can be detected, involving the dispersal of a canid possibly related to *Canis etruscus*, the so-called "wolf-event" (Azzaroli, 1983). Nevertheless, Villafranchian canids were scarcely recorded in French LFAs.

As far as France is concerned, this renewal was possibly more gradual than previously hypothesised, as showed by the hypothesised co-occurrence in MNQ18 faunal complex of taxa that typically occurred in middle Villafranchian and late Villafranchian LFAs. Assemblages belonging to the following Early Pleistocene are poorly represented in France; indeed it is difficult to correlate the French faunas with the classic late Villafranchian ones, such as the Italian FUs.

Starting from the Jaramillo submagnetochronozone and in the following period (around the Early/Middle Pleistocene boundary, currently correlated with OIS 25: Cita & Castradori 1994), a period of cooler and drier conditions (Shackleton 1984, Shackleton & Hall 1984) given rise to a remarkable reconstruction of faunal assemblages and a major community reorganization (see Alberdi et al., 1997; Torre et al., 2001; Palombo, in press). The renewal can be clearly detected in the French faunas belonging to MNQ20.

During the early Middle Pleistocene, phases of climate worsening and periods of increase seasonal variation and aridity favoured a widespread steppe-grass land, while deciduous forests noticeably diminished.

During the Late Pleistocene the French fauna progressively acquired a modern configuration

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### REFERENCES

- Aguilar J.-P., Legendre S., Michaux J. et col. (1997) - Synthesis and correlation tables. In: "European Neogene Mammal Chronology" AGUILAR J.-P., LEGENDRE S., Michaux J. (Eds), 769-805, *Mém. Trav. E.P.H.E., Inst. Montpellier*.
- Agustí J. & Antón M. (2002) - Mammoths Sabertooths, and Hominids - 65 Million Years of Mammalian Evolution in Europe. 313 p., *Columbia University Press*, New York.
- Agustí J., Cabrera L., Garcés M., Krijgsman W., Oms O. & Parés J.M. (2001) - A calibrated mammal scale for the Neogene of Western Europe. State of the art. *Earth-Science Reviews*, **52**, 247-260.
- Alberdi M.T., Azanza B., Cernedo E. & Prado J.L. (1997) - Similarity relationship between Mammal faunas and biochronology from Latest Miocene to Pleistocene in the Western Mediterranean area. *Eclog. Geol. Helvetiae*, **90** (1), 115-132.
- Ambrosetti P. (1967) - Cromerian fauna of the Rome area.

- Quaternaria*, **9**, 267-283.
- Aouraghe H. (1999) - Nouvelle reconstitution du Paléo-environnement par les grands mammifères: les faunes du Pléistocène moyen d'Ornac 3 (Ardèche, France). *L'Anthropologie*, **103** (1), 177-184.
- Argant A. & Crégut-Bonnoure E. (1996) - Famille des Ursidae. In: "Les grands mammifères plio-pléistocènes d'Europe", Guérin C. & PATOU-MATHIS M. (Eds), 167-179, *Masson*, Paris.
- Argant A. (1991) - Carnivores quaternaires en Bourgogne. *Doc. Lab. Géol. Lyon*, **115**, 301 p.
- Azanza Asensio B. (2000) - Los Ciervidae (Artiodactyla, Mammalia) del Mioceno de las Cuencas del Duero, Tajo, Calatayud-Teruel y Levante. *Memorias del Museo Paleontológico de la Universidad de Zaragoza*, **8**, 376 p.
- Azanza B., Nieto M., Soria D. & Morales J. (1997) - El registro neógeno de los Cervoidea (Artiodactyla, Mammalia) de España. In: "Avances en el conocimiento del Terciario Ibérico" CALVO J.P. & MORALES J. (Eds), 41-44, *Universidad Complut. Madrid, Consejo Superior de Investigaciones Científicas*.
- Azzaroli A. (1977) - The Villafranchian Stage in Italy and the Plio-Pleistocene Boundary. *G. Geol.*, **41**, 61-79.
- Azzaroli A. (1979) - Critical remarks on some giant deer (genus *Megaceros* Owen) from the Pleistocene of Europe. *Palaeont. Ital. (new series)*, **71**, 5-16.
- Azzaroli A. (1982) - Remarques sur les subdivisions chronologiques du Villafranchien. *Actes Colloque "Le Villafranchien Méditerranéen"*, Lille 9-10 décembre 1982, **1**, 7-14.
- Azzaroli A. (1983) - Quaternary mammals and the "End-Villafranchian" dispersal event - A turning point in the history of Eurasia. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, **44**, 117-139.
- Azzaroli A. (1992) - The cervid genus *Pseudodama* n.g. in the Villafranchian of Tuscany. *Palaeont. Ital. (new series)*, **79**, 1-41.
- Azzaroli A., Colalongo M.L., Nakagawa H., Pasini G., Rio D., Ruggeri G., Sartori S. & Sprovieri R. (1997) - The Plio-Pleistocene boundary in Italy. In: "The Pleistocene boundary and the beginning of the Quaternary" VAN COUVERING J.A. (Ed.), 141-155, *Cambridge University Press*.
- Azzaroli A., De Giuli C., Ficarelli G. & Torre D. (1988) - Late Pliocene to Early Mid-Pleistocene mammals in Eurasia: Faunal succession and dispersal events. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, **66**, 77-100.
- Bailon S., Deslaux E., Echassoux A., Lacombe F., Moullé P.-E. (2003) - The vertebrates of Vallonet cave continental level (Roquebrune-Cap-Martin, Alpes Maritimes, France): A typical fauna of the second half of Lower Pleistocene in a cold period with contrasted season. *Jornadas temáticas de Arqueología de Andalucía, Granada 3-5 April 2003, Abstracts book*, 13-15.
- Ballesio R. (1985) - Sur l'appartenance systématique des restes du gisement ruscinién du Serrat d'en Vacquer (Roussillon) attribués par Charles Depéret à *Machairodus cultridentis* (Cuvier). *Coll. "Hommage à Charles Depéret"*, *Mus. Hist. Nat. Perpignan*, oct. 1985, abstract, 12, Perpignan.
- Bianucci G., Mazza P., Merola D., Sarti G. & Cascella A. (2001) - The early Pliocene mammal assemblage of Val di Pugna (Tuscany, Italy) in the light of calcareous plankton biostratigraphical data and paleoecological observations. *Riv. Ital. Paleont. Stratigr.*, **107** (3), 425-438.
- Biddittu I., Cassoli P.F., Radicati di Brozolo F., Segre A.G., Segre-Naldini E. & Villa I. (1979) - Anagni a K: Ar dated Lower Middle Pleistocene site, Central Italy: preliminary report. *Quaternaria*, **21**, 53-71.
- Biquard D., Dubar M. & Semah F. (1990) - Paleomagnetic correlation of the Mediterranean Upper Neogene. Biochronology and Villafranchian vertebrates' sites of the Massif Central, France. *Quaternary Res.*, **33**, 241-252.
- Bœuf O. (1990) - Originalité et importance de la faune plio-pléistocène de Chilhoc (Haute Loire, France). *Quartärtaerpäliäontologie*, **8** (28), 13-28.
- Bœuf O. (1997) - A propos de Chilhoc, Senèze, Blassac-la-Gironde (Haute-Loire, France), gisements du Pliocène terminal, leur intérêt biochronologique. In: "European Neogene Mammal Chronology" Aguilar J.-P., LEGENDRE S., Michauxi J. (Eds), 661-668, *Mém. Trav. E.P.H.E., Inst. Montpellier*.
- Bonadonna F.P. & Alberdi M.T. (1987) - *Equus stenonis* Cocchi as a biostratigraphical marker in the Neogene-Quaternary of the Western Mediterranean Basin: consequence on Galerian-Villafranchian chronostratigraphy. *Quaternary Science reviews*, **6**, 59-66.
- Bonifay M.-F. (1969) - Principales formes caractéristiques du quaternaire moyen du sud-est de la France. *Bull. Mus. Anthropol. Préhist. Monaco*, **14**, 49-62.
- Bonifay M.-F. (1971) - Carnivores quaternaires du Sud-Est de la France. *Bull. Mus. natn. Hist. nat.*, sér. C, **21**, 377 p.
- Bonifay M.-F. (1975) - Les Ursidae de la Fage (Corrèze). *Nouv. Arch. Mus. Hist. nat. Lyon*, **13**, 21-28.
- Bonifay M.-F. (1978) - Faunes de transition du Pléistocène moyen de France. *Bull. Mus. Anthropol. Préhist. Monaco*, **22**, 5-15.
- Bonifay M.-F. (1990): Relations between paleoclimatology and Plio-Pleistocene biostratigraphic data in West Europe countries. In: "European Neogene Mammal Chronology" Lindsay E.H., Fahlbush V. & Mein P. (Eds), 475-485, *Plenum Press*, New York.
- Bonifay M.-F. (1992) - Apport des grandes faunes villafranchiennes du Massif Central français dans le cadre général du Plio-Pléistocène. *Proc. 117<sup>e</sup> Congr. nat. soc. sav.*, 55-64.
- Bouchez R., Bruandet J.F., Ma J.-L., Piboule M., Amosse J., Poupeau G., Nickel B. & Rey P. (1986) - Caractérisation et datation d'émail dentaire de Vertébrés par des méthodes radionucléaires. In: "Teeth revisited: proceeding of the VIIth International Symposium on dental morphology, Paris, 1986", Russell D.E., Santoro J.-P. & Sigoneau-Russell D. (Eds.), *Mém. Mus. natn. Hist. nat.*, Paris, sér. C, **53**, 169-176.
- Bouchez R., Lopez Carranza E., Ma J.-L., Amosse J., Piboule M., Cornu A., Diebolt J., Galland D., Rey P., Lumeley de H. & Guérin C. (1984) - Datation par résonance paramagnétique électronique d'émail fossile provenant des sites d'Ayusbamba, Pérou, de Saint-Vallier et de la Caune de l'Arago (France). *1er Symp. internat. Archéologique africaine et Sciences de la Nature appliquées à l'Archéologie, Bordeaux, septembre 1983, Revue Archéométrie*, **8**, 70-79.
- Bourdier F. (1961-1962) - Le bassin du Rhône au Quaternaire - Géologie et Préhistoire. 360 p., 2 vol. *CNRS édit.*, Paris.
- Bravard A. (1828) - Monographie de la Montagne de Perrier et de deux espèces fossiles du genre *Felis*. 146 p. *Dufour et Docagne édit.*, Paris.
- Brugal J.-P. (1992) - Les Bovidés. In: "Les animaux de la Préhistoire entre Provence et Toscane", Crégut-Bonnoure E. (Ed.), 54-60. *Soc. Ed. Sci. nat. Vaucluse édit.*, Avignon.
- Bruijn de H., Daams R., Daxner-Höck G., Fahlbusch V.,



- Ginsburg L., Mein P. & Morales J. (1992) - Report of the RCMNS working group on fossil mammals, Reimsburg 1990. *Newsl. Stratigr.*, **26**, 65-118.
- Caloi L., Palombo M.R. & Petronio C. (1980) - Resti cranici di *Hippopotamus antiquus* (= *H. major*) et *H. amphibius* conservati nel Museo di Paleontologia dell'Università di Roma. *Geologica Romana*, **19**, 91-119.
- Carraro F. (1996) - Revisione del Villafranchiano nell'area - tipo di Villafranca d'Asti. *Il Quaternario*, **9** (1), 5-120
- Chaline J. (1997) - Biostratigraphy and calibrated climatology chronology of the Upper Pliocene and Lower Pleistocene of France. In: "The Pleistocene boundary and the beginning of the Quaternary" Van Couvering J.A. (Ed.), 178-182. *Cambridge University Press*.
- Chaline J., Erbajeva A.E. & Montuire S. (2000) - Upper Pliocene Leporidae (Mammalia, Lagomorpha) from Moutoussé-5 (Haute-Pyrénées, France). *N. Jb. Geol. Paläont. Mh.*, **2**, 93-106.
- Cita M.B. & Castradori D. (1994) - Workshop on marine sections from the Gulf of Taranto (Southern Italy) usable as potential stratotypes for the GSSP of the Lower, Middle and Upper Pleistocene: Il Quaternario, **7** (2), 677-692.
- Clot A., Chaline J., Heintz E., Jammot D., Mourer-Chauviré C. & Rage J.-C. (1976) - Moutoussé 5 (Haute-Pyrénées), un nouveau remplissage de fissure à faune de vertébrés du Pléistocène inférieur. *Geobios*, **9** (4), 511-514.
- Crégut E. (1992) - Les Caprinae (Mammalia, Bovidae) du Pléistocène d'Europe: intérêt biostratigraphique, paléocologique et archéozoologique. *Mém. Soc. géol. France*, **160**, 85-93.
- Crégut E. (2002) - Les Oviprovini, Ovini et Caprini (Mammalia, Artiodactyla, Bovidae, Caprinae) du Plio-Pleistocene d'Europe occidentale: systématique, évolution et biostratigraphie. *Thèse d'Etat, Université Claude-Bernard Lyon 1*, 3 tomes, 306 + 17 p.
- Croizet J.-B. & Jobert A.-C.-G. (1828) - Recherches sur les ossements fossiles du département du Puy-de-Dôme. 224 p. *Thiribaud-Landriot*, Clermont-Ferrand.
- Debard E., Faure M. & Guérin L. (1994) - Stratigraphie du gisement villafranchien moyen de Saint-Vallier (Drôme). *C.R. Acad. Sci. Paris*, **318**, série II, 1283-1286.
- Delpech F. & Prat F. (1980) - Les grands mammifères pléistocènes du sud-ouest de la France. *Bull. Ass. fr. étud. Quater.*, **17**, 268-297.
- Delson E. (1974) - Preliminary review of cercopithecoid distribution in the Circum Mediterranean Region. *Mém. B.R.G.M.*, **78** (1) (*V<sup>e</sup> cong. Néogène méditerranéen-Lyon, 1971*), 131-135.
- Depéret C. & Mayet L. (1911) - Le gisement de Mammifères pliocènes de Senèze (Haute-Loire) et sa faune paléomammalogique. *C.R. Assoc. fr. Avancement Sci. Cong. Dijon*, **1**, 261-263.
- Di Stefano G. & Petronio C. (2003) - Systematics and evolution of the Eurasian Plio-Pleistocene tribe Cervini (Artiodactyla, Mammalia). *Geologica Romana*, **36** (2000-2002), 311-334.
- Dong W. (1996) - Les Cervidae (Artiodactyla) rusciniens (Pliocène) du Languedoc et du Roussillon (France). *Bull. Mus. natn. Hist. nat.*, 4<sup>e</sup> ser., **18**, section C, 133-163.
- Duvernois M.-P. (1990) - Les *Leptobos* (Mammalia, Artiodactyla) du Villafranchien d'Europe Occidentale. *Doc. Lab. Géol. Lyon*, **113**, 213 p.
- Eisenman V. (1984) - Sur quelques caractères adaptatifs du squelette des *Equus* (Mammalia, Perissodactyla) et leurs implication paléocologique. *Bull. Mus. natn. Hist. nat.*, sér. 4, section C, **6** (2), 185-195.
- Eisenman V. (1991) - Les chevaux quaternaires européens (Mammalia, Perissodactyla). Taille, typologie, bio-stratigraphie et taxonomie. *Geobios*, **24** (6), 747-759.
- Eisenmann V. (2003) - Gigantic Horses. In: "Advances in Paleontology - Hen to Panta", papers in honour of Radulescu C. & Samson P.M., 31-40, Bucharest.
- Eisenmann V., Crégut E. & Moigne A.-M. (1985) - *Equus mosbachensis* et les grands Chevaux de la Caune de l'Arago et de Lunel-Viel: crâniologie comparée. *Bull. Mus. nat. Hist. nat.*, 4<sup>e</sup>me série, **7** (2), Section C, 157-173.
- Fauquette S., Guiot J. & Suc J.-P. (1998) - A method for climatic reconstruction of the Mediterranean Pliocene using pollen data. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, **144**, 183-201.
- Fauquette S., Suc J.-P., Guiot J., Diniz F., Feddi N., Zheng Z., Bessais E. & Drivaliari A. (1999) - Climate and biomes in the West Mediterranean area during the Pliocene. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, **152**, 15-36.
- Faure M. (1985) - Les hippotames quaternaires non-insulaires d'Europe Occidentale. *Nouv. Arch. Mus. Hist. nat. Lyon*, **23**, 13-79.
- Faure M., Guérin C. & Moguillon-Douillet A. (2002) - Sur la campagne 2002 de prospection thématique et sondage dans le gisement villafranchien supérieur de Senèze (commune de Domeyrat, Haute-Loire). *D.R.A.C., Clermont Ferrand*, 67 p.
- Fernandez P. (2001) - Etude paléontologique et archéozoologique des niveaux d'occupation moustériens au Bau de l'Aubesier (Monieux, Vaucluse): implications biochronologiques et paléontologiques. *Thèse troisième cycle, Université Claude-Bernard Lyon 1*, n° 158, 3 tomes, 306 p.
- Fortelius M., Mazza P. & Sala B. (1993) - *Stephanorhinus* (Mammalia: Rhinocerotidae) of western European Pleistocene, with a revision of *S. etruscus* (Falconer, 1868). *Palaeont. Ital.*, **80**, 63-155.
- Fosse P. (1992) - Acquisition et exploitation des ressources animales au Très Ancien Paléolithique: l'exemple de Soleihac (Haute-Loire, France). *117 Congrès National des Sociétés Savantes (Moyenne montagne), Clermont-Ferrand*, **2**, 43-54.
- Fosse P. (1996) - La grotte n°1 de Lunel-Viel (Hérault, France): repaire d'Hyènes du Pléistocène moyen. *Paleo*, **8**, 47-79.
- Geraads D. (1990) - Contribution des cervidés à la chronologie des débuts de l'occupation humaine en Europe occidentale. *Quaternaire*, **3/4**, 167-174.
- Ginsburg L. (1975) - Etude paléontologique des Vertébrés pliocènes de Pont-de-Gail (Cantal). *Bull. Soc. Géol. Fr.*, **17** (5), 752-759.
- Gliozzi E., Abbazzi L., Ambrosetti P., Argenti P., Azzaroli A., Caloi L., Capasso Barbato L., Di Stefano G., Esu D., Ficcarelli G., Girotti O., Kotsakis T., Masini F., Mazza P., Mezzabotta C., Palombo M.R., Petronio C., Rook L., Sala B., Sardella R., Zanolza E. & Torre D. (1997) - Biochronology of selected Mammals, Molluscs, Ostracods from the Middle Pliocene to the Late Pleistocene in Italy. The state of the art. *Riv. It. Paleont. Stratigr.*, **103** (3), 369-388.
- Gromolard G. & Guérin C. (1980) - Mise au point sur *Parabos corderi* (De Christol), un bovidé (Mammalia, Artiodactyla) du Pliocène d'Europe occidentale. *Geobios*, **13** (5), 471-755.
- Gromolard G. (1981) - Les grands Bovidae (Mammalia,

- Artiodactyla) du Pliocène d'Europe occidentale : biostratigraphie, paléoneurologie, systématique, évolution, paléocologie. *Thèse Univ. Claude-Bernard-Lyon 1*, 231 p.
- Groves C.-P. (1983) - Phylogeny of the living species of rhinoceros. *Zeitschr. f. zoo. Systematic u. Evolutionsforsch*, **21**, 293-313.
- Guérin C. (1973) - Les trois espèces de Rhinocéros (Mammalia, Perissodactyla) du gisement Pléistocène moyen des Abîmes de la Fage à Noailles (Corrèze). *Nouv. Archiv. du Muséum d'hist. Nat. Lyon*, **11**, 55-84.
- Guérin C. (1980) - Les Rhinocéros (Mammalia, Perissodactyla) du Miocène terminal au Pléistocène Supérieur en Europe Occidentale. *Doc. Lab. Géol. Lyon*, **79**, 3 tomes, 1185 p.
- Guérin C. (1982) - Première biozonation du Pléistocène européen, principal résultat biostratigraphique de l'étude des Rhinocerotidae (Mammalia, Perissodactyla) du Miocène terminal au pléistocène supérieur de l'Europe occidentale. *Geobios*, **15** (4), 593-598.
- Guérin C. (1990) - Biozones or Mammal Units? Methods and Limits in Biochronology. In: "European Neogene Mammal Chronology" Lindsay E.H., Fahlbush V. & Mein P. (Eds), 119-130. *Plenum Press*, New York.
- Guérin C. (1996a) - Superordre des Proboscidiens. In: "Les grands mammifères plio-pléistocènes d'Europe", Guérin C. & Patou-Mathis M. (Eds), 141-153. *Masson*, Paris.
- Guérin C. (1996b) - Ordre des Périssodactyles. In: "Les grands mammifères plio-pléistocènes d'Europe", Guérin C. & Patou-Mathis M. (Eds), 107-136. *Masson*, Paris.
- Guérin C. (1996c) - Famille des Hippopotamidae. In: "Les grands mammifères plio-pléistocènes d'Europe", Guérin C. & Patou-Mathis M. (Eds), 44-47. *Masson*, Paris.
- Guérin C. (1998) - Mammifère, datations et paléoenvironnements en préhistoire. *Quaternaire*, **9** (4), 249-260.
- Guérin C., Dewolf Y. & Lautridou J.-P. (2003) - Révision d'un site paléontologique célèbre: Saint-Prest (Chartres, France). *Geobios*, **36**, 55-82.
- Guérin C. & Faure M. (2002) - The Mid-Villafranchian mammals of Saint-Vallier (Drôme, France). *1st International Workshop on Late Plio/Pleistocene extinction and evolution in the Palearctic. The vatera Fauna, Polichnitos (Lesbos, Grèce)*, *Ann. géol. Pays hell.*, **39**.
- Guérin C. & Mein P. (1971) - Les principaux gisements mammifères miocènes et pliocènes du domaine rhodanien. *Doc. Lab. Géol. Univ. Lyon, H.S.* 131-170.
- Guérin C. & Patou-Mathis M. (Eds) (1996) - Limites et problèmes de chronologie. In: "Les grands mammifères plio-pléistocènes d'Europe", Guérin C. & Patou-Mathis M. (Eds), 1-11. *Masson*, Paris.
- Guth C. (1973) - Chiljac et Blassac-la-Girondie, deux gisements villafranchiens de la vallée de l'Allier. *Coll. Internat. Paléont.*, *Centre Nat. Rech. Sci., Paris, Problèmes actuels Paléontologie et Evolution, Vertébrés*, 627-630, Paris.
- Guth C., Bœuf O., Latreille G. & Méon H. (1979) - Etudes paléontologique, sédimentologique et palynologique du gisement pléistocène inférieur de Chiljac III (Haute Loire). *R.A.S.T., 7<sup>e</sup> Réunion annuelle des Sciences de la Terre, Lyon, Soc. Géol.* 244 p.
- Guth C. & Chavaillon J. (1985) - Découverte, en 1984, de nouveaux outils paléolithiques à Chiljac III (Haute-Loire). *Bull. Soc. préhist. fr.*, **82** (2), 56-64.
- Hadjouis D. (1990) - *Megaceroides algericus* (Lydekker, 1890), du gisement des Phacochères (Alger, Algérie). Etude critique de la position systématique de *Megaceroides*. *Quaternaire*, **3/4**, 247-258.
- Heintz E. (1970) - Les Cervidés villafranchiens de France et d'Espagne. *Bull. Mus. natn. Hist. nat.*, Paris, sér. C, **22**, 303 p.
- Heintz E. (1971) - Présence de *Gazella* (Bovidae, Artiodactyla, Mammalia) dans les sables marins de Montpellier, Hérault, France. *Bull. Mus. natn. Hist. nat.*, 2<sup>e</sup> sér., **42** (2), 1334-1336.
- Heintz, E. & Dubar M. (1981) - Place et signification des dépôts villafranchiens de Moustiers-Ségriès et faune de Mammifères de Cornillet (Alpes de Haute-Provence). *Bull. Mus. natn. Hist. nat.*, 4e sér., **3**, section C (2), 363-397.
- Heintz, E. & Poplin F. (1980) - *Alces carnutorum* (Laugel, 1862) du Pléistocène de Saint-Priest (France). Systématique et évolution des Alcinés. *Quartär-paläontologie*, **4**, 105-122.
- Heintz, E., Guérin C., Martin P. & Prat F. (1974) - Principaux gisements villafranchiens de France: listes faunistiques et biostratigraphie. *Mém. B.R.G.M.*, **78** (1) (V<sup>e</sup> cong. Néogène méditerranéen-Lyon, 1971), 411-417.
- Howell F.C. & Petter G. (1980) - The *Pachycrocuta* and *Hyaena* lineages (Plio-Pleistocene and extant of the Hyaenidae). Their relationships with miocene Ictitheres: *Palhyaena* and *Hyaenictitherium*. *Geobios*, **13** (4), 579-623.
- Kahlke H.-D. (1952) - Der altpleistocäne *Verticornis*-Kreis und die Frage der Entstehung der Riesenhirsche (*Megaceros*). *Hallesches Jahrb. Mit. Erdgeschichte*, **1**, 174-179.
- Kahlke, R.-D. (2001) - Schädelreste von Hippopotamus aus dem unterpleistozän von unter massfeld. In: "Das Pleistozän von Untermassfeld bei meiningen (Thüringen)", Kahlke, R.-D. (Ed.), 483-500, *Römisch-Germanisches Zentralmuseum Mainz*.
- Lacombat F. (2003) - Etudes des rhinocéros du Pléistocène de l'Europe méditerranéenne et du Massif Central. Paléontologie, phylogénie et biostratigraphie. *Thèse troisième cycle, Mus. natn Hist. Nat.*: 509 p.
- Legendre S. & Lévêque F. (1997) - Etalonnage de l'échelle biochronologique mammalienne du Paléogène d'Europe occidentale: vers une intégration à l'échelle globale. In: "European Neogene Mammal Chronology" Aguilar J.-P., Legendre S., Michauxi J. (Eds), 461-473. *Mém. Trav. E.P.H.E., Inst. Montpellier*.
- Lindsay E.H., Opdyke N.D. & Johnson N.M. (1980) - Pliocene dispersal of the horse *Equus* and Late Cenozoic mammalian dispersal events. *Nature*, **287**, 135-138.
- Lister A. (1990) - Critical reappraisal of the Middle Pleistocene Deer species "*Cervus*" *elaphoides* Kahlke. *Quaternaire*, **3/4**, 175-192.
- Lister A. (1993) - The stratigraphical significance of deer species in the Cromer Forest-bed Formation. *J. Quat. Sc.*, **8** (2), 95-108.
- Lumeley de H., Kahlke H.D., Moigne A.M. & Moullé P.E. (1988) - les faunes de grands mammifères de la grotte du Vallonnet. Roquebrune-Cap-martin, Alpes-maritimes. *L'Anthropologie*, **92**, 465-496.
- Lumeley de H., Fournier A., Abdessadok S., Perrenoud C., Khatib S. (2000) - Cadre stratigraphique, géochronologique et paléoclimatologique du Pléistocène inférieur et moyen dans le Midi méditerranéen de la France d'après des formations quaternaires de sites préhistoriques: Le Vallonnet, la Caune de l'Arago, Terra-Amata, Orgnac 3, La Baume-Bonne, Le Lazaret. *Coll. Int. "Les premiers habi-*

- tants de l'Europe*", *Tautavel 15 Avril 2000*, 15-17.
- Martin P. (1973) - Trois nouvelles espèces de Caninae (Canidae, Carnivora) des gisements plio-villafranchiens d'Europe. *Doc. Lab. Géol. Fac. Sci. Lyon*, **57**, 87-96.
- Martinez Navarro B. & Rook L. (2003) - Evolution of African wild dogs. The site of Venta Micena. *Jornadas tematicas de Arqueologia de Andalucia, Granada 3-5 April 2003, Abstracts book*, 38.
- Mazza P. (1991) - Interrelations between Pleistocene hippopotami of Europe and Africa. *Boll. Soc. Paleont. Ital.*, **30** (2), 153-186.
- Mazza P. (1995) - New evidence on the Pleistocene Hippopotamuses of Western Europe. *Geologica Romana*, **31**, 61-241.
- Mazza P., Bertini A. & Magi M. (in press) - The Late Pliocene Site of Poggio Rosso (Central Italy): Taphonomy and Paleoenvironment. *Palaiois*.
- Mazzini M., Borselli V., Cioppi E. & Napoleone G. (2000) - Poggiorosso: un importante arricchimento delle faune villafranchiane a vertebrati del Valdarno Superiore, di età prossima al limite Plio-Pleistocene. *Boll. Soc. Paleont. Ital.*, **39**, 381-388.
- Mein P. (1975) - Résultats du groupe de travail des vertébrés: bizonation du Néogène méditerranéen à partir des Mammifères. *Report Activity RCMNS working groups*, 78-81, Bratislava.
- Mein P. (1990) - Updating of MN zones. In: "European Neogene Mammal Chronology" Lindsay E.H., Fahlbush V. & Mein P. (Eds), 73-90. *Plenum Press*, New York.
- Mein P. (1998) - Biochronologie et phases de dispersion chez les Vertébrés cénozoïques. *Bull. Soc. géol. France*, **170** (2), 195-204.
- Méon H., Ballesio R., Guérin C. & Mein P. (1980) - Approche climatologique du Néogène supérieur (Tortonien à Pléistocène Moyen Ancien) d'après les faunes et les flores d'Europe occidentale. *Mém. Mus. natn. Hist. nat.*, Paris, sér. B, **27**, 182-195.
- Michaux J. (1969) - Les gisements de Vertébrés de la région montpelliéraine, 3. Gisements pliocènes. *Bull. B.R.G.M.*, section I, **2** (1), 31-37.
- Moigne A.-M., Palombo M.R., Belda V., Djamilia Heriech-Briki D., Kacimi S., Lacombat F., de Lumley A.M., Moutoussamy J., Rivals F., Quiles J., Agnès Testu A. (in press) - Les faunes de grands mammifères de la Caune de l'Arago (Tautavel) dans le cadre biochronologique des faunes du Pléistocène moyen Italien. *L'Anthropologie*.
- Moigne A.-M. & Valensi P. (2000) - Les faunes du Pléistocène supérieur dans le Midi de la France: Terra-Amata, Orgnac 3, La Baume-Bonne, Le Lazaret. *Coll. Int. "Les premiers habitants de l'Europe"*, *Tautavel 15 Avril 2000*, 59-60.
- Monguillon-Douillet A. (2000) - Les carnivores du site plio-pleistocène de Chilhac (Haute-Loire, France) - Etude paléontologique, biochronologique, paléoécologique et taphonomique. *Mémoire de D.E.A. "Quaternaire: Géologie, Paléontologie humaine, préhistoire"*, Paris: 95 p.
- Moullé, P.-E. (1998) - Les grandes mammifères de la grotte du Vallonet (Roquebrune-cap-martin): Synthèse des études antérieures et nouvelles déterminations. *Bull. Musée Anthropol. Préhist.* Monaco, **39**, 29-36.
- Moullé, P.-E., Echassoux A., Moigne A.-M., Palombo M.R., Caloi L., Kahlke R.-D., Vekue A. & Lordkipanidzé D. (2000) - Les faunes de la fin du Pléistocène inférieur de la grotte du Vallonet (Alpes-Maritimes, France), de Redicicoli (Latium, Italie), de Untermassfeld (Allemagne) et de Akhalkalaki (Georgie): l'horizon biostratigraphique du Vallonet. *Coll. Int. "Les premiers habitants de l'Europe"*, *Tautavel 15 Avril 2000*: 50-51.
- Mourer-Chauviré C. (1972) - Etude de nouveaux restes de Vertébrés provenant de la carrière Fournier à Châtillon-Saint-Jean (Drôme)-Arctiodactyles, chevaux et oiseaux. *Bull. Ass. fr. étud. Quater.*, **4**, 271-302.
- Mourer-Chauviré C., Ballesio R., Beden M., Chaline J., David L., Guérin C., Hugueney M., Jammot D., Mein P., Rage J.-C. & Vilain R. (1975) - Conclusions générales sur les faunes de l'aven I des Abîmes de la Fage (Corrèze). *Nouv. Arch. Mus. Hist. nat. Lyon*, **13**, 123-129.
- Palombo M.R. (in press) - Guilds of large mammals from the Pliocene to the Late Pleistocene in Italian peninsula. *Homage Prof. E. Aguirre, Universidad Complutense, Madrid*.
- Napoleone G., Azzaroli A. & Mazzini M. (2003) - Magnetostratigraphic significance of the end-Pliocene age of the new found locality of Poggio Rosso in the Upper Valdarno, for dating its late Villafranchian faunas. *Rivista Italiana di Paleontologia e Stratigrafia*, **108** (3), 479-492.
- Palombo M.R. (in press) - Guild of large Mammals from the Pliocene to the Late Pleistocene in the Italian peninsula. In Baquedano, E. & Rubio, S. (eds). *Homenaje a Emiliano Aguirre*. Zona Paleontologica, Museo Arqueológico Regional, Madrid.
- Palombo M.R., Azanza B., Alberdi M.T. (2003) - Italian mammal biochronology from Latest Miocene to Middle Pleistocene: a multivariate approach. *Geologica Romana*, **36**, (2000-2002), 335-368.
- Palombo M.R., Milli S. & Rosa C. (2004) - Remarks on the late Middle Pleistocene biochronology of the mammalian faunal complexes of the Campagna Romana. *Geologica Romana*.
- Pareto M. (1865) - Note sur la subdivision que l'on pourrait établir dans les terrains de l'Apennin septentrional. *Bulletin de la Société Géologique de France*, série 2, **22**, 210-277.
- Partridge T.C. (1997) - Reassessment of the position of the Plio-Pleistocene boundary: is there a case for lowering it to the Gauss-Matuyama palaeomagnetic reversal? *Quaternary International*, **40**, 5-10.
- Petronio C. (1986) - Nuovi resti di ippopotamo del Pleistocene medio-inferiore dei dintorni di Roma e problemi di tassonomia e filogenesi del gruppo. *Geologica Romana*, **25**, 63-72.
- Petronio C. & Sardella R. (1999) - Biochronology of the Pleistocene mammal fauna from Ponte Galeria (Rome) and remarks on the Middle Galerian faunas. *Riv. It. Paleont. Strat.*, **105**, 155-164.
- Poidevin J.L., Cantagrel J.M. & G.U.E.R.P.A. (1984) - Un site unique du Plio-Pleistocene en Europe: le plateau de Perrier (Puy-de-Dôme) - Confrontation des données volcanologiques, stratigraphiques et paléontologiques. *Rev. Sc. Nat. d'Auvergne*, **50**., 87-95.
- Pomel A. (1846) - Quelques nouvelles considérations sur la paléontologie de l'Auvergne. *Bull. Soc. Géol. Fr.*, sér. 2, **3**., 198-231.
- Poplin F. (1972) - Nouveaux restes de Mégacéros (*Megaceros* cf. *giganteus*, Cervidae, Mammalia) à Châtillon-Saint-Jean (Drôme). *Bull. Ass. fr. étud. Quater.*, **4**: 239-247.
- Portis A. (1920) - Elenco delle specie dei Cervicorni fossili in Roma e attorno Roma. *Boll. Soc. Geologica Romana*, **39**, 132-139.
- Prat F. (1968) - Recherches sur les Equidés pléistocènes en



- France. *Thèse Doctorat Etat Fac. Sci. Bordeaux*, 692 p.
- Prévot M. & Dalrymple G.B. (1970) - Un bref épisode de polarité géomagnétique normale au cours de l'époque inverse Matuyama. *C.R. Acad. Sci. Paris*, **271**, ser. D, 2221-2224.
- Roger S., Coulon C., Thouveny N., Férand G., Van Velzen A., Fauquette S., Cochemé J.J., Prévot M. & Verosub K.L. (2000) -  $^{40}\text{Ar}/^{39}\text{Ar}$  dating of a tephra layer in the Pliocene Senèze maar lacustrine sequence (French Massif Central): constraint on the age of the Reunian-Matuyama transition and implication on paleoenvironmental archives. *Earth and Planetary Science Letters*, **138**, 431-440.
- Rook L. & Torre D. (1996) - The last Villafranchian - early Galerian small dogs of the Mediterranean area. *Acta zoologica Cracoviensia*, **39** (1), 427-434.
- Rook L. (1993) - I cani dell'Eurasia dal Miocene superiore al Pleistocene medio. *Thèse Dott. ricerca, Univ. Cons. Modena, Bologna, Firenze, Roma "La Sapienza"*, 130 p., Firenze.
- Schaub S. (1941) - Die ober Pliocene Säugetierfauna von Senèze (Haute Loire, France) und ihre verteilungsgeschichtliche stellung. *Eclogae geol. Helv.*, **36**, 270-289.
- Shackleton, M.J. (1984) - Oxygen isotope evidence for Cenozoic climate change. In: *Fossils and Climate*. (P. Brenchley, Ed.), John Wiley, New York: 27-34.
- Shackleton N.J. (1995) - New Data on the Evolution of Pliocene Climatic Variability. - In: "Paleoclimate and Evolution, with Emphasis on Human Origins" Vrba E.S., Denton G.H., Partridge T.C. & Burckle L.H. (Eds), 242-248. *New Haven and London* (Yale University Press, 1996).
- Shackleton, M.J. (1997) - The Deep-Sea Sediment Record and the Pliocene-Pleistocene Boundary. *Quaternary International*, **40**, 33-35.
- Shackleton M.J. & Hall M.A. (1984) - Oxygen and carbon isotope stratigraphy of Deep Sea Drilling Project Hole 552A: Plio-Pleistocene glacial history. In: *Initial Reports of the Deep Sea Drilling Project*, 81 U.S. Government Print Off. (D.G. Robert, and D. Schnitker, Eds.), Washington, 599-609.
- Suc J.-P., Bertini A., Combourieu-Nebout N., Diniz F., Leroy S., Russo-Ermolli E., Zheng Z., Bessais E. & Ferrier J. (1995) - Structure of West Mediterranean vegetation and climate since 5.3 Ma. *Acta Zoologica Cracoviensia*, **38** (1), 3-16.
- Thouveny N. & Bonifay E. (1984) - New chronological data on European Plio-Pleistocene faunas and hominid occupation sites. *Nature*, **308**, 355-358.
- Torre D., Ficarelli G., Masini F., Rook L. & Sala B. (1992) - Mammal dispersal events in the early Pleistocene of Eastern Europe. *Courier Forsch.-Inst. Senckenberg*, **153**, 51-58.
- Torre D., Abbazzi L., Bestini A., Fanfani F., Ficarelli G., Masini F., Mazza P. & Rook L. (2001) - Structural changes in Italian Late Pliocene-Pleistocene large mammal assemblages. *Bollettino Società Paleontologica Italiana*, **40** (2), 303-306.
- Torres T. (1984) - Ursidos del Pleistoceno Holoceno de la Peninsula Iberica. *Thèse Doct. C.S.I.C. Madrid*.
- Turner A. & Antón M. (1997) - The big cats and their fossil relatives. *Columbia University Press*, 234 p., New York.
- Valensi P. & Abbassi M. (1998) - Reconstitution de paléoenvironnements quaternaires par l'utilisation de divers méthodes sur une communauté de mammifères - Application à la grotte du Lazaret. *Quaternaire*, **9** (4), 291-302.
- Valensi P. (2001) - The Elephants of Terra Amata open air site (Lower Paleolithic, France). In: "La Terra degli Elefanti - The World of Elephants" Cavarretta G., Gioia P., Mussi M. & Palombo M.R. (Eds), 260-264. *Atti del 1° Congresso Internazionale, Roma, 16-20 Ottobre 2001, Consiglio Nazionale delle Ricerche, Rome*.
- Valli A.M.F. (2001) - Le gisement villafranchien moyen de Saint-Vallier (Drôme): nouvelles données paléontologiques (Cervidae, Bovinae) et taphonomiques. *Doc. Lab. Géol. Lyon*, **153**, 275 p.
- Van Dam J.A. (2001) - The Upper Miocene Mammal record from the Teruel-Alfambra region (Spain). The MN system and continental Stage/Age concepts discussed. *Journal of Vertebrate Paleontology*, **21**(2), 367-385.
- Van der Made J. (1999) - Ungulates from Atapuerca TD6. *J. Hum. Evol.*, **37**, 389-413.
- Vekua A.K. (1986) - The lower Pleistocene fauna of Mammals of Akhalkalaki. *Ac. Sci. Rép. Géorgie*, 207 p.
- Viret J. (1954) - Le loess à bancs durcis de Saint-Vallier (Drôme) et sa faune de Mammifères villafranchiens. *Nouv. Archiv. Mus. hist. Nat. Lyon*, **4**, 1- 266.
- Vislobokova I., Sotnikova M. & Dodonov A. (2001) - Late Miocene-Pliocene Mammalian faunas of Russia and neighboring countries. *Boll. Soc. Pal. It.*, **40** (2), 307-313.
- Walsh S.L. (1998) - Fossil datum and paleobiological event terms, Paleostratigraphy, Chronostratigraphy and the definition of Land Mammal "Age" boundaries. *J. Vert. Paleont.*, **18** (1), 150-179.
- Werdelin L. (1981) - Annales Zoologici Fennici. *Ann. Zool. Fenn.*, **18**, 37-71.

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## APPENDIX

## Some systematic remarks

The systematics and taxonomy of the Latest Villafranchian and Early - Middle Galerian small fossil dogs is controversial. In Rook and Torre's opinion (1996) "at least two different phyletic lineages would be present, one in the Mediterranean - leading from *Canis arnensis* to *Canis* aff. *arnensis* - the second in the north and central Eurasia - leading from *Canis etruscus* to *Canis mosbachensis*", moreover by some authors the later taxon have been considered as subspecies of *Canis lupus*. Although, the holotype of *Canis mosbachensis* seems to be more related to *C. arnensis* than to *Canis etruscus* or *Canis lupus*. Taking into consideration these problems, in this paper we prefer the ascribed the Middle Galerian small dogs to *Canis* sp. ex gr. *C. mosbachensis*/*C. arnensis*. It is also worth noting that *Alopex* sp. probably first appeared in the Arago Cave (Moigne et al., in press).

As Felidae concerns, *Lynx* systematic follows Werdelin (1981). As the felids from Le Vallonet and Arago cave are concerned the hypothesis that they belong to species different from *P. pardus* cannot be ruled out.

The systematic and taxonomy of the Middle Pleistocene caballine horses were discussed a long time and experts disagree. Taking into account these taxonomic problems and doubts, we included all the Middle Pleistocene *Equus* species of the "caballin" lineage in "*Equus ferus* sensu lato" (according to CINZ, the name "*caballus*" cannot be retained because of erected by Linnaeus for domestic equids, even if we are conscious that this attribution cannot be considered formally correct. Moreover, for the taxonomy of the French horses see also Eisenman (1984, 1991, 2003), Eisenman et al. (1985) and Prat (1968).

The taxonomy of Villafranchian and Galerian rhinoceros follows Groves (1983), as pointed out by Fortelius et al., 1993 and, more recently, by Lacombe (2003; also see the references therein).

The taxonomy of the European representatives of the genus *Hippopotamus* has been discussed inter alios by Caloi et al. (1980); Faure (1985), Mazza (1991, 1995), Petronio (1986), Vekua (1986), Kahlke (2001); the authors disagree about it. Apart from the proposed taxonomic settings, European Pleistocene hippopotamuses were without doubt characterized by a marked polymorphism, which owes much to ecophenotypes. It is however possible to define two groups on the basis of cranial features: the *Hippopotamus* ex gr. *H. antiquus* (slightly similar to the species *H. gorgops*) - that lowest occurred in the Italian latest Early Pleistocene and in Europe for most of the early Middle Pleistocene - and the *Hippopotamus* ex gr. *H. amphibius* (similar to the living species), certainly present in the Mediterranean area since the late early Middle Pleistocene (Fontana Ranuccio LFA, Italy).

The systematic and taxonomy of the Pliocene-Early and Middle Pleistocene middle-sized deer from European sites (ascribed to *Pseudodama* genus by Azzaroli 1992) are still undefined because the authors widely disagree (cfr. Van der Made, 1999; Valli, 2001; Di Stefano & Petronio, 2003; Palombo et al., 2003 and references therein). The medium-sized cervids actually can be considered separate in generic ranking from the representative of the genus *Dama*. However, their taxonomy seems to be rather complex and still unclear; more than one lineage should be present in this group even if their belonging to the same genus cannot be ruled out. Hence, pending conclusive new data, we prefer to group them in the

genus "*Pseudodama*": we do not use "*Cervus*" to avoid confusion with other taxa, like "*Cervus*" *perrieri*, which belongs to a clearly different genus.

The taxonomy of large deer belonging to the Megacerini tribe has been discussed a long time and the authors are still far from reaching a consensus (e.g. Ambrosetti, 1967; Azzaroli, 1979; Geraads, 1990; Lister, 1993, and references therein). There is a quite good agreement in considering the Pleistocene European megacerine as belonging to two different lineages: the *Megaloceros giganteus* and the *verticornis-solihacus* groups. The authors are divided between "*Praemegaceros*", an actually very poorly defined Portis (1920) genus, and "*Megaceroides*", erected for "*Cervus*" *algericus*, a particular species, whose features are not representative of the European giant deer belonging to "*verticornis-solihacus*" group (see also Hadjouis, 1990). Moreover, we have to keep in mind the name "*Orthogonoceros*", which has been erected by Kahlke (1952) for some Süsselborn Megacerini. In this paper we provisionally use the name "*Praemegaceros*" because it is still widely used by several authors.

The systematic and taxonomy of the French bovids follow CRÉGUT (1992, 2000), GROMOLARD (1981) and DUVERNOIS (1990).

## French localities

## MONTPELLIER, SABLES MARINS LITTORAUX (HÉRAULT)

Michaux, 1969; Guérin & Mein, 1971; Heintz, 1971; Delson, 1974; Dong, 1996

Age: MN14 (Ruscinian, Early Pliocene)

**Large Mammal Fauna:** *Dolichopithecus ruscinensis*, *Mesopithecus monspessulanus*, *Viverra peparaxi*, Hyaenidae indet., Machairodontini indet., *Felis christoli*, *Ursus minimus*, *Agriotherium insigne*, *Lutra affinis*, *Meles genèvevauxi*, *Plesiogulo monspessulanus*, *Anancus arvernensis*, *Pliohyrax graecus*, *Tapirus arvernensis*, *Hipparion crassum*, *Dicerorhinus megarhinus*, *Korhynchoerus provincialis*, *Cervavitus cauvieri*, *Paracervulus australis*, *Paracervulus christoli*, *Parabos cordieri*, *Gazella* sp..

## MONTPELLIER, FORMATION DU PALAIS DU JUSTICE (HÉRAULT)

Michaux, 1969; Guérin & Mein, 1971; Heintz, 1971; Delson, 1974; Dong, 1996

Age: MN14 (Ruscinian, Early Pliocene)

**Large Mammal Fauna:** *Dolichopithecus ruscinensis*, *Macaca sylvanus priscus*, *Mesopithecus monspessulanus*, Hyaenidae indet., Machairodontini indet., *Anancus arvernensis*, *Pliohyrax graecus*, *Tapirus arvernensis*, *Hipparion crassum*, *Dicerorhinus megarhinus*, *Korhynchoerus provincialis*, *Cervavitus cauvieri*, *Paracervulus australis*, *Parabos cordieri*.

## CELLENEUVE (HÉRAULT)

Guérin, 1980

**Age:** MN14 (Ruscinian, Early Pliocene)

**Large Mammal Fauna:** *Mesopithecus monspessulanus*, *Anancus arvernensis*, *Dicerorhinus megarhinus*, *Parabos cordieri*.

TRÉVOUX (AIN)

Guérin, 1980

**Age:** MN14 (Ruscinian, Early Pliocene)

**Large Mammal Fauna:** *Ursus minimus*, *Anancus arvernensis*, *Tapirus arvernensis*, *Dicerorhinus megarhinus*, *Paracervulus australis*, *Parabos cordieri*.

PONT-DE-GAIL (CANTAL)

Ginsburg, 1975; Guérin, 1980

**Age:** MN14 (Ruscinian, Early Pliocene)

**Large Mammal Fauna:** *Hipparion crassum*, *Dicerorhinus* cf. *megarhinus*, *Paracervulus australis*, *Parabos cordieri*.

SAINT-LAURENT-DES-ARBRES (GARD)

Guérin, 1980; Alberdi pers. comm.

**Age:** MN14 (Ruscinian, Early Pliocene)

**Large Mammal Fauna:** *Hipparion crassum*, *Anancus arvernensis*, *Dicerorhinus megarhinus*, *Korhynchoerus provincialis*, Cervidae indet., *Parabos cordieri*.

PERPIGNAN (SERRAT D'EN VACQUER)

Ballesio, 1985; Rook, 1993; Bruijn de et al., 1992; Dong, 1996

**Age:** MN15 (Ruscinian, Early Pliocene)

**Large Mammal Fauna:** *Dolichopithecus ruscinensis*, *Mesopithecus monspessulanus*, *Viverra pepratxi*, *Pachycrocuta pyrenaica*, *Dinofelis diastemata*, *Homotherium* sp., *Felis* aff. *maniculata*, *Lynx issiodorensis*, *Ursus minimus*, *Nyctereutes donnezani*, “*Canis*” *Michauxi*, *Eucyon adoxus*, *Anancus arvernensis*, *Mammuthus (Zygodon) borsoni*, *Tapirus arvernensis minor*, *Hipparion crassum*, *Dicerorhinus megarhinus*, *Stephanorhinus miquelcrusafonti*, *Orycteropus depereti*, *Sus minor*, *Korhynchoerus provincialis*, *Paracervulus perpignanensis*, “*Cervus*” *pyrenaicus*, “*Cervus*” *rusciniensis*, *Alephis lyrix*, *Gazella* aff. *borbonica*.

AUTREY (HAUTE-SAÔNE)

Guérin, 1980; Gromolard & Guérin, 1980

**Age:** MN15 (Ruscinian, Early Pliocene)

**Large Mammal Fauna:** *Anancus arvernensis*, *Mammuthus (Zygodon) borsoni*, *Tapirus arvernensis*, *Hipparion crassum*, *Dicerorhinus megarhinus*, *Alephis lyrix*.

VIALETTE (HAUTE-LOIRE)

Heintz et al. 1974

**Age:** MN16a (early Villafranchian, Middle Pliocene)

**Large Mammal Fauna:** *Paradolichopithecus* sp., *Nyctereutes megamastoides*\*, “*Canis*” sp. 1, *Agriotherium insigne*, *Ursus minimus*, ?*Pachycrocuta perrieri*, *Lynx issiodorensis*, *Mammuthus (Zygodon) borsoni*, *Anancus arvernensis*, *Tapirus arvernensis*, *Stephanorhinus jeanvireti*, *Stephanorhinus* cf. *s. etruscus*\*, *Procapreolus cusanus*, *Croizetoceros ramosus ramosus*, “*Pseudodama*” *pardinensis*, “*Cervus*” *perrieri*, *Arvernocervus ardei*, *Leptobos* sp.\*.

**Observations:**\* Lacombe, personal communication to M.R. Palombo, 2003.

LES ETOUAIRES-PERRIER (PUY-DE-DÔME)

Heintz et al., 1974; Duvernois, 1990

**Age:** MN16a (early Villafranchian, Middle Pliocene)

**Large Mammal Fauna:** *Nyctereutes megamastoides*, ?*Vulpes alopecoides*, *Canis* sp. 1, *Baranogale antica*, *Enhydriactis ardea*, *Aonyx bavardi*, *Ursus minimus*, *Pachycrocuta perrieri*, *Chasmaporthetes lunensis*, *Lynx issiodorensis*, *Acinonyx pardinensis*, ?*Homotherium crenatidens*, *Megantereon cultridens*, *Mammuthus (Zygodon) borsoni*, *Anancus arvernensis*, *Tapirus arvernensis*, *Stephanorhinus jeanvireti*, *Stephanorhinus etruscus*, *Sus minor*, *Procapreolus cusanus*, *Croizetoceros ramosus ramosus*, “*Pseudodama*” *pardinensis*, “*Cervus*” *perrieri*, *Arvernocervus ardei*, *Gazella borbonica*, *Pliotragus ardeus*, *Leptobos elatus*, *Leptobos bravardi*.

**Observations:** After Poidevin et al. (1984) the age of this site would be about 2.5 Ma, and the fauna listed above would be a mixt from several levels.

CHAGNY (SAÔNE-ET-LOIRE)

Bourdier, 1961-1962; Heintz & Poplin, 1980; Duvernois, 1990

**Age:** MN16-17 (early-middle Villafranchian, Middle Pliocene)

**Large Mammal Fauna:** *Ursus minimus*, *Homotherium crenatidens*, *Pachycrocuta perrieri*, *Mammuthus (Zygodon) borsoni*, *Anancus arvernensis*, *Mammuthus meridionalis*, *Tapirus arvernensis*, *Stephanorhinus etruscus*, “*Cervus*” *perrieri*, *Gazella borbonica*, *Leptobos elatus*.

**Observations:** for the biochronological problem of this site see Heintz & Poplin (1980) but also Guérin & Faure (2002).

ROCCANEYRA (PUY-DE-DÔME)

Heintz et al., 1974; Duvernois, 1990, Binquard et al., 1990; Alberdi, pers. comm.

**Age:** MN16b (middle Villafranchian, Late Pliocene)

**Large Mammal Fauna:** *Nyctereutes megamastoides*, *Chasmaporthetes lunensis*, *Lynx issiodorensis*, *Anancus* cf. *A. arvernensis*, *Hipparion rocinantis*, *Equus stenonis*, *Eucladoceros ctenoides vireti*, *Leptobos elatus*, *Gazellospira torticornis*, ?*Procamptoceras brivatense*, *Gazella borbonica*.

## SAINT-VALLIER (DRÔME)

Viret, 1954; Bouchez et al., 1984, 1986; Debard et al., 1994; Guérin, 1998; Valli, 2001; Guérin & Faure, 2002

**Age:** MN17a (middle Villafranchian, Late Pliocene)

**Large Mammal Fauna:** *Macaca sylvanus florentinus*, *Nyctereutes megamastoides*, *Vulpes alopecoides*, *Baranogale antica*, *Enhydriactis ardea*, *Aonyx bavardi*, *Meles thoralis*, *Ursus etruscus*, *Pachycrocuta perrieri*, *Chasmaporthetes lunensis*, *Lynx issiodorensis*, *Viretailurus schaubi*, *Acinonyx pardinensis*, *Homotherium crenatidens*, *Megantereon cultridens*, *Anancus arvernensis*, *Mammuthus meridionalis*, *Stephanorhinus etruscus*, *Equus stenonis vireti*, *Sus strozzii*, *Croizetoceros ramosus medius*, "Pseudodama" rhenanus valliensis, *Eucladoceros ctenoides vireti*, *Gazella borbonica*, *Gazellospira torticornis*, *Gallogoral meneghini*, *Leptobos elatus merlai*.

## PARDINES (PUY-DE-DÔME)

Heintz et al., 1974; Bonadonna & Alberdi, 1987; Duvernois, 1990

**Age:** MN17a (middle Villafranchian, Late Pliocene)

**Large Mammal Fauna:** *Nyctereutes megamastoides*, *Chasmaporthetes lunensis*, *Lynx issiodorensis*, *Homotherium crenatidens*, *Megantereon cultridens*, *Anancus arvernensis*, *Stephanorhinus etruscus*, *Equus major*, *Equus stenonis* cf. *E. s. vireti*, *Croizetoceros ramosus medius*, "Pseudodama" rhenanus valliensis, *Eucladoceros ctenoides vireti*, *Gazella borbonica*, *Gazellospira torticornis*, *Leptobos* sp. (*L. etruscus* vel *L. merlai*).

## SAINT-VIDAL (HAUTE-LOIRE)

Heintz et al., 1974; Bonadonna & Alberdi, 1987

**Age:** MN17a (middle Villafranchian, Late Pliocene)

**Large Mammal Fauna:** *Anancus arvernensis*, *Mammuthus meridionalis*, *Stephanorhinus etruscus*, *Equus stenonis vireti*, *Croizetoceros ramosus medius*, *Gazella borbonica*.

## LA ROCHE LAMBERT (HAUTE-LOIRE)

Heintz et al., 1974; Bonadonna & Alberdi, 1987

**Age:** MN17a (middle Villafranchian, Late Pliocene)

**Large Mammal Fauna:** *Anancus arvernensis*, *Stephanorhinus etruscus*, *Equus stenonis vireti*, *Croizetoceros ramosus medius*, *Eucladoceros ctenoides vireti*, *Gazella borbonica*.

## CORNILLET (ALPES DE HAUTE PROVENCE)

Heintz & Dubar, 1981; Bonadonna & Alberdi, 1987; Duvernois, 1990

**Age:** MN17a (middle Villafranchian, Late Pliocene)

**Large Mammal Fauna:** *Nyctereutes megamastoides*,

*Pachycrocuta perrieri*, *Stephanorhinus etruscus*, *Equus stenonis vireti*, *Croizetoceros ramosus*, "Pseudodama" rhenanus, *Eucladoceros ctenoides*, *Gazella borbonica*, cf. *Gazellospira torticornis*, *Leptobos etruscus*.

## LE COUPET (HAUTE-LOIRE)

Heintz et al., 1974; Bonadonna & Alberdi, 1987; Duvernois, 1990

**Age:** MN17b (middle Villafranchian, Late Pliocene)

**Large Mammal Fauna:** *Homotherium crenatidens*, *Anancus arvernensis*, *Mammuthus meridionalis*, *Stephanorhinus etruscus*, *Equus bressanus*, *Equus stenonis vireti*, *Croizetoceros ramosus minus*, "Pseudodama" rhenanus valliensis, *Eucladoceros ctenoides senezensis*, *Gazellospira torticornis*, *Leptobos furtivus*.

## CHILHAC 2 (HAUTE-LOIRE)

Guth, 1973; Guth et al., 1979; Bœuf, 1990, 1997; Monguillon-Douillet, 2000

**Age:** MN17b (middle Villafranchian, Late Pliocene)

**Large Mammal Fauna:** *Nyctereutes megamastoides*, *Canidae* indet., *Vulpes* cf. *V. alopecoides*, *Ursus etruscus*, *Pachycrocuta perrieri*, *Megantereon cultridens*, *Anancus arvernensis chilhiacensis*, *Mammuthus meridionalis*, *Stephanorhinus etruscus*, *Equus stenonis guthi*, *Croizetoceros ramosus*, "Pseudodama" rhenanus, *Eucladoceros ctenoides vireti*, *Gazellospira torticornis*, *Gallogoral meneghini*.

**Observations:** Chilhac 3 is also known; its fauna is poorer than the one of Chilhac 2 (but *Homotherium crenatides* has been recorded; Monguillon-Douillet, 2000). Its age is different of that of Chilhac II (Guth & Chavaillon, 1985).

## MONTOUSSÉ 5 (HAUTE-PYRÉNÉES)

Clot et al., 1976; Heintz & Poplin, 1980; Chaline et al., 2000

**Age:** MN18 (late Villafranchian, Latest Pliocene)

**Large Mammal Fauna:** *Macaca sylvanus florentinus*, *Canis* aff. *C. etruscus*, *Ursus* cf. *U. etruscus*, *Enhydriactis* sp., *Martes* sp., *Mustela palerminea*, *Mustela* cf. *M. praenivalis*, *Felis sylvestris lunensis*, *Lynx issiodorensis*, *Machairodontini* indet., *Stephanorhinus etruscus*, "Pseudodama" rhenanus, *Cervalces gallicus*, ?*Procampoceras brivatense*.

## SENÈZE (HAUTE-LOIRE)

Dépéret & Mayet, 1911; Heintz, 1970, 1971; Prévot & Dalrympe, 1970; Roger et al., 2000; Faure et al., 2002

**Age:** MN18 (late Villafranchian, Latest Pliocene)

**Large Mammal Fauna:** *Macaca sylvanus* cf. *M. s. florentinus*, *Paradolichopithecus avernensis*, *Nyctereutes megamastoides*, ?*Vulpes alopecoides*, *Canis senesensis*, *Ursus etruscus*, *Pachycrocuta perrieri*, *Acinonyx pardinensis*, *Homotherium crenatidens*, *Megantereon cultridens*, *Mammuthus meridionalis*, *Stephanorhinus etruscus*, *Equus bressanus*, *Equus stenonis senezensis*, *Sus strozzii*, *Croizetoceros ramosus minus*,

“*Pseudodama*” *rhenanus philisi*, *Eucladoceros ctenoides senezensis*, *Cervalces gallicus*, *Gazellospira torticornis*, *Megalovis latifrons*, *Gallogoral meneghini*, *Procamptoceras brivatense*, *Pliotragus ardeus*, *Leptobos furtivus*, *Leptobos etruscus*.

PEYROLLES (HAUTE-LOIRE)

Heintz, 1970; Heintz et al., 1974; Duvernois, 1990

**Age:** MN19 (late Villafranchian, Early Pleistocene)

**Large Mammal Fauna:** *Stephanorhinus etruscus*, “*Pseudodama*” *rhenanus perolensis*, *Eucladoceros tetraceros*, *Leptobos* sp..

BLASSAC-LA-GIRONDIE (VALLÉE DE L'ALLIER)

Heintz et al., 1974; Bonadonna & Alberdi, 1987; Duvernois, 1990

**Age:** MN19 (late Villafranchian, Early Pleistocene)

**Large Mammal Fauna:** *Canis* aff. *C. etruscus*, *Ursus etruscus*, *Pachycrocuta perrieri*, *Mammuthus meridionalis*, *Stephanorhinus etruscus*, *Equus* cf. *E. major*, *Equus stenorhis senezensis*, “*Pseudodama*” *rhenanus perolensis*, *Eucladoceros tetraceros*, *Leptobos etruscus*.

LA SARTANETTE, PORCHE D'ENTRÉE (GARD)

Duvernois, 1990; Crégut, 2002

**Age:** MN19 (late Villafranchian, Early Pleistocene)

**Large Mammal Fauna:** *Ursus etruscus*, *Pachycrocuta brevirostris*, *Lynx pardina spelaea*, *Homotherium* aff. *H. crenatidens*, *Stephanorhinus etruscus*, *Equus stenorhis*, *Leptobos etruscus*.

LE VALLONNET (ALPES-MARITIMES)

de Lumley et al., 1988, 2000; Moullé, 1998; Moullé et al., 2000; Crégut, 2002; Bailon et al., 2003.

**Age:** MN20 (early Galerian, late Early Pleistocene)

**Large Mammal Fauna:** *Macaca sylvanus florentinus*, «*Xenocyon*» *lycaonoides*, *Vulpes praeglacialis*, *Ursus* aff. *U. deningeri*, *Pachycrocuta brevirostris*, *Meles meles*, *Acinonyx pardinensis*, *Lynx pardina spelaea*, *Panthera* ex gr. *P. gombaszoegensis*, *Panthera pardus*, *Homotherium crenatidens*, *Mammuthus meridionalis*, *Stephanorhinus hunsheimensis*, *Equus suessenbornensis*, *Equus altidens*, *Sus* cf. *S. strozzi*, “*Pseudodama*” *nestii vallonnetensis*, “*Praemegaceros*” cf. “*M.*” *verticornis*, *Bison schoetensacki*, *Hemitragus* sp., *Ovibovinae* indet., *Caprinae* indet.

SAINZELLES (HAUTE-LOIRE)

Guérin, 1980; Méon et al., 1980; Bonadonna & Alberdi, 1987; Lister, 1990; Brugal, 1992

**Age:** MN20 (early Galerian, late Early Pleistocene)

**Large Mammal Fauna:** *Canis* ex gr. *C. mosbachensis/C. arnensis*, *Pachycrocuta brevirostris*, *Lynx pardina spelaea*, *Homotherium crenatidens*, *Mammuthus meridionalis*, *Stephanorhinus hunsheimensis*, *Equus altidens*, *Hippopotamus* ex gr. *H. antiquus*, *Cervidae* indet. (middle-sized), *Megacerini* indet., *Bison schoetensacki*.

SOLEILHAC (HAUTE LOIRE)

Bonifay, 1971; Guérin, 1980; Thouveny & Bonifay, 1984; Bonadonna & Alberdi, 1987; Lister, 1990; Fosse 1992; Crégut 2002; Lacombat, unpublished data

**Age:** MN20 (early Galerian, late Early Pleistocene)

**Large Mammal Fauna:** *Canis* ex gr. *C. mosbachensis/C. arnensis*, *Vulpes* sp., *Ursus deningeri*, *Mammuthus meridionalis*, *Elephas (Palaeoloxodon) antiquus*, *Stephanorhinus hunsheimensis*, *Equus altidens*, *Equus* cf. *E. suessenbornensis*, *Hippopotamus* ex gr. *H. antiquus*, ?*Cervus elaphus*, “*Praemegaceros*” *solilhacus*, *Capreolus capreolus suessenbornensis*, *Bison schoetensacki*, *Hemitragus orientalis*.

SAINT-PREST (CHARTRES)

Guérin, 1980; Lister, 1990, Guérin et al. 2003

**Age:** MN20 (early Galerian, late Early Pleistocene)

**Large Mammal Fauna:** *Pachycrocuta brevirostris*, *Mammuthus meridionalis depereti*, *Stephanorhinus hunsheimensis*, *Equus* cf. *altidens*, *Hippopotamus* ex gr. *H. antiquus*, *Cervidae* indet., *Cervalces carnutorum*, *Megacerini* indet. (?*Megaloceros savini*), cf. “*Praemegaceros*” *verticornis*, *Bison schoetensacki*.

**Observations:** After Guérin et al (2003) among the middle sized cervids two taxa are present belonging to *Cervus elaphus* and *Dama* respectively. Among the large cervid remains, an incomplete mandible could be tentatively ascribed to “*Praemegaceros*” *verticornis* due to its important pachyostosis (see Guérin et al 2003 for a discussion). More problematic is the taxonomic attribution of the fragment of skull (frontal and basal portion of the left antler), whose first tine shows an elliptical section (Guérin et al, 2003, Fig. 9).

DURFORT (GARD)

Guérin, 1980; Lister, 1990; Brugal, 1992

**Age:** MN20 (?early Galerian, late Early Pleistocene)

**Large Mammal Fauna:** *Canidae* indet., *Mammuthus meridionalis*, *Stephanorhinus hunsheimensis*, *Hippopotamus* ex gr. *H. antiquus*, ?“*Pseudodama rhenanus perolensis*”, *Bison schoetensacki*.

L'ESCALE À SAINT-ESTÈVE-JANSON (BOUCHES DU RHÔNE)

Bonifay, 1971; Crégut, 2002

**Age:** MN22 (middle Galerian, early Middle Pleistocene)

**Large Mammal Fauna:** *Macaca sylvanus sylvanus*, *Canis* ex gr. *C. mosbachensis/C. arnensis*, *Cuon* cf. *C. stehlini*, *Vulpes*



*praeglacialis*, *Vulpes vulpes*, *Ursus denigeri*, *Mustela palerminea*, *Gulo gulo*, *Panthera leo fossilis*, *Hyaena prisca*, *Lynx pardina spelaea*, *Stephanorhinus kirchbergensis*, “*Praemegaceros*” *solilhacus*, *Hemitragus bonali*.

NAUTIÈRE (GERS)

Guérin, 1980; Brugal, 1992

**Age:** MN22 (middle Galerian, early Middle Pleistocene)

**Large Mammal Fauna:** *Canis* ex gr. *C. mosbachensis/C. arnensis*, *Ursus* cf. *U. denigeri*, *Ursus thibetanus*, *Homotherium* ex gr. *H. latidens*, Elephantidae indet., *Stephanorhinus hunsheimensis*, *Equus suessenbornensis*, *Hippopotamus* ex gr. *H. antiquus*, *Cervus* cf. *C. elaphus*, *Capreolus capreolus suessenbornensis*, Megacerini indet., *Bison schoetensacki*.

LUNEL-VIEL, GROTTES N°1 (HÉRAULT)

Fosse, 1996

**Age:** MN23a (middle Galerian, early Middle Pleistocene)

**Large Mammal Fauna:** *Canis lunellensis*, *Cuon priscus*, *Vulpes vulpes*, *Meles thoralis*, *Mustela palerminea*, *Lutra* sp., *Ursus* cf. *U. denigeri*, *Hyaena prisca*, *Crocota crocuta*, *Panthera pardus*, *Felis sylvestris sylvestris*, *Lynx pardina spelaea*, *Equus ferus*, *Equus hydruntinus*, *Sus* cf. *S. scrofa*, *Capreolus capreolus suessenbornensis*, *Cervus elaphus*, “*Eucladoceros mediterraneus*”, *Bos primigenius*, *Bison* cf. *B. schoetensacki*.

VERCHIZEUIL (SAÔNE-ET-LOIRE)

Argant, 1991

**Age:** MN23a (middle Galerian, early Middle Pleistocene)

**Large Mammal Fauna:** *Cuon priscus*, *Vulpes vulpes*, *Meles meles*, *Gulo gulo*, *Ursus denigeri*, *Ursus thibetanus*, *Hyaena prisca*, *Felis* sp., *Stephanorhinus hemitoechus*, *Equus ferus*, Cervidae indet., *Cervus elaphus*, *Capreolus capreolus*, *Bos primigenius*.

CAUNE DE L'ARAGO CM I (PYRÉNÉES)

de Lumley et al., 2000; Crégut, 2002

**Age:** MN23a (middle Galerian, early Middle Pleistocene)

**Large Mammal Fauna:** *Canis* ex gr. *C. mosbachensis/C. arnensis*, *Vulpes praeglacialis*, *Cuon priscus*, *Ursus denigeri*, *Ursus arctos*, *Lynx pardina spelaea*, *Panthera leo ssp*, *Panthera* cf. *P. pardus*, *Stephanorhinus hemitoechus*, *Equus ferus*, *Cervus elaphus*, *Dama clactoniana*, *Rangifer tarandus*, *Hemitragus bonali*, *Ovis ammon antica*, *Bison schoetensacki*.

PECH DE L'AZÉ, COUCHE 9 (DORDOGNE)

Delpech & Prat, 1980

**Age:** MN23 (middle Galerian, early Middle Pleistocene)

**Large Mammal Fauna:** *Canis lunellensis*, *Ursus denigeri*,

*Ursus arctos*, *Lynx pardina spelaea*, Elephantidae indet., *Stephanorhinus* sp., *Equus ferus*, *Cervus elaphus*, *Capreolus* sp., *Rangifer tarandus*, Megacerini indet., *Bos primigenius*, *Bison* sp..

PECH DE L'AZÉ, COUCHE 9 (DORDOGNE)

Delpech & Prat, 1980

**Age:** MN23 (middle Galerian, early Middle Pleistocene)

**Large Mammal Fauna:** *Canis lunellensis*, *Ursus denigeri*, *Meles meles*, *Lynx pardina spelaea*, *Crocota crocuta*, *Stephanorhinus kirchbergensis*, *Equus ferus*, *Sus scrofa*, *Cervus elaphus*, *Dama* sp., *Capreolus* sp., *Rangifer tarandus*, Megacerini indet., *Bos primigenius*, *Bison* sp., *Hemitragus bonali*.

COMBE GRENAL (DORDOGNE)

Grégut, 2002

**Age:** MN23 (middle/late Galerian, early Middle Pleistocene)

**Large Mammal Fauna:** Canidae indet., *Vulpes vulpes*, *Martes* sp., *Ursus arctos*, *Ursus* sp., *Crocota crocuta*, *Lynx pardina spelaea*, *Stephanorhinus* sp., *Equus ferus*, *Sus scrofa*, *Cervus elaphus*, *Rangifer tarandus*, *Bos primigenius*, *Bison* sp., *Capra* sp., *Hemitragus bonali*.

CAUNE DE L'ARAGO CM II (PYRÉNÉES)

de Lumley et al., 2000; Crégut, 2002

**Age:** ?MN23b (?late Galerian, early Middle Pleistocene)

**Large Mammal Fauna:** *Meles meles*, *Canis* ex gr. *C. mosbachensis/C. arnensis*, *Cuon priscus*, *Vulpes vulpes*, *Ursus denigeri*, *Ursus arctos*, *Felis sylvestris sylvestris*, *Lynx pardina spelaea*, *Panthera leo spelaea*, *Stephanorhinus hemitoechus*, *Equus ferus*, *Cervus elaphus*, *Dama clactoniana*, *Rangifer tarandus*, *Praeovibos priscus*, *Hemitragus bonali*, *Ovis ammon antiiqua*, *Bison* sp..

CAUNE DE L'ARAGO CM III (PYRÉNÉES)

de Lumley et al., 2000; Crégut, 2002

**Age:** MN23b (late Galerian, early Middle Pleistocene)

**Large Mammal Fauna:** *Mustela palerminea*, *Meles meles*, *Canis* ex gr. *C. mosbachensis/C. arnensis*, *Cuon priscus*, *Vulpes vulpes*, *Ursus denigeri*, *Ursus arctos*, *Felis sylvestris sylvestris*, *Lynx pardina spelaea*, *Panthera leo spelaea*, *Panthera pardus*, Elephantidae indet., *Stephanorhinus hemitoechus*, *Equus ferus*, *Cervus elaphus*, *Dama clactoniana*, *Rangifer tarandus*, *Praeovibos priscus*, *Hemitragus bonali*, *Ovis ammon antiiqua*, *Rupicapra* sp., *Bison priscus*.

GROTTE D'ALDÈNE, COUCHE K (HÉRAULT)

Grégut, 2002

**Age:** MN23b (late Galerian, early Middle Pleistocene)

**Large Mammal Fauna:** *Macaca sylvanus sylvanus*, *Ursus denigeri*, *Ursus thibetanus*, *Panthera leo spelaea*, *Crocota crocuta*, *Stephanorhinus hunsheimensis*, *Equus ferus*, *Cervus elaphus*, *Hemitragus bonali*.

ORGNAC 3 (ARDÈCHE)

Aouraghe, 1999; de Lumley et al., 2000; Moigne & Valensi, 2000; Moigne, pers. comm.

**Age:** MN23b (late Galerian, early Middle Pleistocene)

**Large Mammal Fauna:** *Macaca sylvanus sylvanus*, *Canis* ex gr. *C. mosbachensis*/*C. arnensis*, *Vulpes vulpes*, *Ursus denigeri*, *Ursus thibetanus*, *Lynx pardina spelaea*, *Felis sylvestris sylvestris*, *Panthera leo spelaea*, *Panthera* cf. *P. pardus*, *Crocota crocuta*, *Elephas (Palaeoxodon)* cf. *E. antiquus*, *Equus ferus*, *Stephanorhinus hemitoechus*, *Sus scrofa*, *Cervus elaphus*, *Dama clactoniana*, *Hemitragus bonali*, *Bos primigenius*, *Bison priscus*.

BRUGES (PRÈS DE BORDEAUX)

Guérin, 1980; Crégut pers. comm.

**Age:** ?MN23b (late Galerian, early Middle Pleistocene)

**Large Mammal Fauna:** *Ursus arctos*, *Ursus thibetanus*, *Lynx pardina spelaea*, *Elephas (Palaeoxodon)* cf. *E. antiquus*, *Stephanorhinus hemitoechus*, *Sus scrofa*, *Cervus elaphus*, *Capreolus capreolus*.

PECH DE L'AZÉ, COUCHE 9 (DORDOGNE)

Delpech & Prat, 1980

**Age:** ?MN24 (early Aurelian, late Middle Pleistocene)

**Large Mammal Fauna:** *Canis lupus*, *Ursus denigeri*, *Ursus arctos*, *Martes* sp., *Mustela putorius*, *Lynx pardina spelaea*, *Panthera leo spelaea*, *Panthera pardus*, *Crocota crocuta*, Elephantidae indet., *Stephanorhinus kirchbergensis*, *Equus ferus*, *Sus scrofa*, *Cervus elaphus*, *Capreolus* sp., *Rangifer tarandus*, Megacerini indet., *Bos primigenius*, *Bison* sp., *Hemitragus bonali*.

TERRA AMATA (ALPES MARITIMES)

de Lumley et al., 2000; Valensi, 2001; Crégut, 2002

**Age:** MN24 (early Aurelian, late Middle Pleistocene)

**Large Mammal Fauna:** *Ursus* sp., *Elephas (Palaeoxodon)* cf. *E. antiquus*, *Stephanorhinus hemitoechus*, *Sus scrofa*, *Cervus elaphus*, *Bos primigenius*, *Hemitragus bonali*.

ABÎMES DE LA FAGE (CORRÈZE)

Mourer-Chouviré et al., 1975; Crégut, 2002

**Age:** MN24 (early Aurelian, late Middle Pleistocene)

**Large Mammal Fauna:** *Canis lupus*, *Vulpes vulpes*, ?*Ursus deningeri*, *Meles meles*, *Gulo gulo*, *Mustela erminea*, *Mustela nivalis*, *Mustela eversmanni*, *Panthera leo spelaea*, *Mam-*

*muthus* ex gr *M. trogotherii*/*M. primigenius*, *Equus* cf. *E. ferus*, *Stephanorhinus kirchbergensis*, *Stephanorhinus hemitoechus*, *Coelodonta antiquitatis*, *Cervus elaphus*, *Dama clactoniana*, *Capreolus capreolus capreolus*, *Rangifer tarandus*, *Megaloceros* cf. *M. giganteus*, *Hemitragus bonali*, *Bison* cf. *B. priscus*.

**Observations:** *Ursus deningeri* have been recognised on the basis of fragmentary teeth and few metapodials (Bonifay, 1975), however the latter do not seem to present the typical morphology of such a species as described in Torres (1984).

CARRIÈRE FOURNIER, CHÂTILLON-SAINT-JEAN (DRÔME)

Mourer-Chouviré, 1972; Poplin 1972; Brugal, 1992

**Age:** MN24 (early Aurelian, late Middle Pleistocene)

**Large Mammal Fauna:** *Canis lupus*, *Vulpes vulpes*, *Ursus spelaeus*, *Ursus arctos*, *Crocota crocuta*, *Mammuthus* ex gr *M. trogotherii*/*M. primigenius*, *Coelodonta antiquitatis*, *Equus* cf. *E. ferus*, *Equus hydruntinus*, *Cervus elaphus*, *Megaloceros* cf. *M. giganteus*, *Bison priscus*.

MONTOUSSÉ 1 (HAUTE-PYRÉNÉES)

Chaline et al., 2000

**Age:** MN24 (early Aurelian, late Middle Pleistocene)

**Large Mammal Fauna:** *Canis lupus*, *Vulpes vulpes*, *Ursus* sp., *Stephanorhinus hemitoechus*, *Equus ferus*, *Cervus elaphus*, *Capreolus capreolus capreolus*, *Bison* cf. *B. priscus*.

GROTTE DES CÈDRES (VAR)

Crégut, 2002

**Age:** MN24 (early Aurelian, late Middle Pleistocene)

**Large Mammal Fauna:** *Canis lupus*, *Vulpes vulpes*, *Ursus arctos*, *Ursus* cf. *U. spelaeus*, *Ursus thibetanus*, *Felis sylvestris sylvestris*, *Panthera leo spelaea*, *Sus scrofa*, *Cervus elaphus*, *Capreolus capreolus capreolus*, *Dama* cf. *D. dama*, *Rangifer tarandus*, *Bos primigenius*, *Bison* sp., *Hemitragus cedrensis*, *Rupicapra* sp..

CAUNE DE L'ARAGO, COMPLEXE SOMMITAL (PYRÉNÉES)

de Lumley et al., 2000; Crégut, 2002

**Age:** MN24 (early Aurelian, late Middle Pleistocene)

**Large Mammal Fauna:** *Macaca sylvanus sylvanus*, *Meles meles*, *Canis lupus*, *Vulpes vulpes*, *Ursus spelaeus*, *Ursus arctos*, *Felis sylvestris*, *Lynx* sp., *Panthera pardus*, ?*Crocota crocuta*, *Equus ferus*, *Sus scrofa*, *Cervus elaphus*, *Hemitragus cedrensis*, *Capra* aff. *C. caucasica*, *Bison priscus*.

BIACHE-SAINT-WAAST (PAS DE CALAIS)

Guérin, 1980

**Age:** MN24 (early Aurelian, late Middle Pleistocene)

**Large Mammal Fauna:** *Canis lupus*, *Ursus* sp., *Panthera leo spelaea*, Elephantidae indet., *Equus ferus*, *Equus hydruntinus*, *Stephanorhinus kirchibergensis*, *Stephanorhinus hemitoechus*, *Sus scrofa*, *Cervus elaphus*, *Capreolus capreolus capreolus*, *Rangifer tarandus*, *Megaloceros giganteus*, *Bos primigenius*.  
ABRI-SUARD (CHARENTE).  
Guérin, 1980

**Age:** MN24 (early Aurelian, late Middle Pleistocene)

**Large Mammal Fauna:** *Canis lupus*, *Vulpes vulpes*, *Alopex lagopus*, *Ursus spelaeus*, *Meles meles*, *Panthera leo spelaea*, *Crocota crocota*, *Mammuthus primigenius*, *Equus ferus*, *Equus hydruntinus*, *Coelodonta antiquitatis*, *Stephanorhinus kirchibergensis*, *Sus scrofa*, *Cervus elaphus*, *Capreolus capreolus capreolus*, *Rangifer tarandus*, *Megaloceros giganteus*, *Bos* vel *Bison*, *Capra ibex*, *Rupicapra* sp., *Saiga tatarica*.

LEVALLOIS (RÉGION PARISIENNE)

Guérin, 1980

**Age:** MN24 (early Aurelian, late Middle Pleistocene)

**Large Mammal Fauna:** *Elephas (Paleoloxodon) antiquus*, *Mammuthus primigenius*, *Stephanorhinus hemitoechus*, *Equus ferus*, *Equus hydruntinus*, *Hippopotamus* ex gr. *H. amphibius*, *Sus scrofa*, *Cervus elaphus*, *Megaloceros giganteus*, *Bos* vel *Bison*.

BAUME DE GONVILLARS (BEÇANSON)

Guérin, 1980

**Age:** MN24 (early Aurelian, late Middle Pleistocene)

**Large Mammal Fauna:** *Canis lupus*, *Ursus spelaeus*, *Panthera leo spelaea*, *Stephanorhinus kirchibergensis*, *Equus ferus*, *Sus scrofa*, *Cervus elaphus*, *Capreolus capreolus capreolus*, *Bison priscus*.

BAU DE L'AUBESIER, COUCHE I-K (VAUCLUSE)

Fernandez, 2001; Crégut, 2002

**Age:** MN24 (early Aurelian, late Middle Pleistocene)

**Large Mammal Fauna:** *Stephanorhinus hemitoechus*, *Equus ferus*, *Cervus elaphus*, *Capreolus capreolus capreolus*, *Dama* cf. *D. dama*, *Rangifer tarandus*, *Megaloceros* cf. *M. giganteus*, *Bos primigenius*, *Hemitragus cedrensis*.

BAU DE L'AUBESIER, COUCHE 1-H (VAUCLUSE)

Fernandez, 2001; Crégut, 2002

**Age:** MN24 (early Aurelian, late Middle Pleistocene)

**Large Mammal Fauna:** *Ursus arctos*, *Equus ferus*, *Sus scrofa*, *Cervus elaphus*, *Capreolus capreolus capreolus*, *Dama* cf. *D. dama*, *Rangifer tarandus*, *Megaloceros* cf. *M. giganteus*, *Bos primigenius*, *Hemitragus cedrensis*.

BAU DE L'AUBESIER, COUCHE 4 (VAUCLUSE)

Fernandez, 2001; Crégut, 2002

**Age:** MN24 (early Aurelian, late Middle Pleistocene)

**Large Mammal Fauna:** *Canis lupus*, *Ursus arctos*, *Panthera leo spelaea*, *Equus* sp., *Sus scrofa*, *Cervus elaphus*, *Capreolus capreolus capreolus*, *Dama* cf. *D. dama*, *Rangifer tarandus*, *Megaloceros* cf. *M. giganteus*, *Bos primigenius*, *Capra* cf. *C. caucasica*, *Rupicapra* sp..

GROTTE DU LAZARET CII (NICE)

Guérin, 1980; Valensi & Abbassi, 1998; Crégut, 2002

**Age:** MN24 (early Aurelian, late Middle Pleistocene)

**Large Mammal Fauna:** *Canis lupus*, *Vulpes vulpes*, *Meles meles*, *Ursus arctos*, *Lynx pardina spelaea*, *Panthera leo spelaea*, *Panthera pardus*, *Equus ferus*, *Stephanorhinus hemitoechus*, *Cervus elaphus*, *Dama clactoniana*, *Capreolus capreolus capreolus*, *Rangifer tarandus*, *Megaloceros giganteus*, *Bos* vel *Bison*, *Capra ibex*, *Rupicapra* sp..

GROTTE DU LAZARET CIII (NICE)

Guérin, 1980; Valensi & Abbassi, 1998; Crégut, 2002

**Age:** MN24 (early Aurelian, late Middle Pleistocene)

**Large Mammal Fauna:** *Canis lupus*, *Vulpes vulpes*, *Meles meles*, *Ursus arctos*, *Ursus spelaeus*, *Lynx pardina spelaea*, *Felis sylvestris sylvestris*, *Panthera leo spelaea*, *Panthera pardus*, *Elephas (Paleoloxodon) antiquus*, *Equus ferus*, *Stephanorhinus hemitoechus*, *Coelodonta antiquitatis*, *Cervus elaphus*, *Dama clactoniana*, *Capreolus capreolus capreolus*, *Rangifer tarandus*, *Megaloceros giganteus*, *Bos primigenius*, *Bison priscus*, *Capra ibex*, *Rupicapra* sp..

