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Mammal Biochronology at the end of Late Villafranchian (Early Pleistocene): Pirro Faunal Unit

by

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With 4 text-figures and 1 table

Zusammenfassung

Fauna Einheiten sind im Moment das einzig wichtige Instrument für die Unterteilung und Charakterisierung des Späten Villafranchium (zwischen 1,6 und 1,1 Ma), ein Zeitraum, der die Pirro Nord Fauna und Pirro Fauna-Einheit umfasst. Einige erste Vorkommen, unter anderem *Theropitecus, Equus altidens* und *Bison degiulii* und vor allem der Entwicklungsstand von *Allophaiomys*, sind sehr nützlich, um die kurzen zeitlichen Abstände darzustellen, in welchen diese Fauneneinheit weiter unterteilt werden kann und um die Synchronität der biochronologischen Daten der Wirbeltierfrauna mit den Steinwerkzeugen aus den Karstfüllungen des Apricena-Gebietes (Foggia, Süditalien) zu vergleichen.

Schlüsselwörter: Spätes Villafranchium – große Säugetiere – kleine Säugetiere – Biochronologie

Summary

Faunal Units represent, at the moment, the sole important instrument to subdivide and characterize the Late Villafranchian (between 1.6 and 1.1 Ma), a time interval that comprises the Pirro Nord fauna and Pirro Faunal Unit. Some first occurrences, among which *Theropitecus, Equus altidens* and *Bison degiulii*, and, above all, the evolutionary degree of *Allophaiomys* are very useful to outline the brief temporal intervals in which this Faunal Unit can be further subdivided and to assess the synchrony of the vertebrate fauna biochronologic data with the lithic tools recovered in the karstic filling of the Apricena (Foggia, Southern Italy) area.

Keywords: Late Villafranchian - large mammals - small mammals - biochronology

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Biochronological studies based on the alternation of mammal faunas are just a different point of view of the biostratigraphic idea of "assemblage zone". Using this criterion fossil remains of mammals "presumably" living in areas surrounding the depositional / recovery basin are studied. Their palaeoecological, palaeoethological consistency and, above all, their evolutionary degrees are observed, obtaining this way, a succession of "instantaneous" Local Faunas (L.F.) that were, most probably, living in different temporal intervals in the observed areas.

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A Local Fauna, having a representative number of taxa and, possibly, of occurrences of bioevents is selected as characteristic of a Faunal Unit (F.U.), namely an ensemble of Local Faunas with similar features, bioevents and taxa that embodies a time interval. An ecologically homogeneous set of F.Us. is a Mammal

Article

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AMPHIBIA	AVES	MAMMALIA
Salamandridae	Treskiornithidae	Soricidae
<i>Lissotriton vulgaris</i> group	Geronticus eremita	Petenyia hungarica
Mesotriton cf. M. alpestris	Anatidae	Asoriculus aff. A. thenii
Pelobatidae	Anser albifrons	Sorex bor
Pelobates sp.	Anser sp.	Crocidura kornfeldi
Bufonidae	Branta bernicla	Crocidura sp.
Bufo bufo	Tadorna ferruginea	Erinaceidae
Bufo viridis	Anas penelope vel Anas clypeata	Erinaceus praeglacialis
Hylidae	Anas clypeata	Talpidae
Hyla arborea group	Anas crecca vel Anas quequedula	Talpa sp.
lanidae	Anas sp.	Miniopteridae
Pelophylax sp.	Aythya sp.	Miniopterus degiulii
	Oxyura sp.	Miniopterus schreibersii
	Falconidae	Vespertilionidae
	Falco subbuteo	Myotis blythii
	Falco peregrinus	Myotis capaccinii
	Phasianidae	Rhinolophidae
	Alectoris rufa	Rhinolophus ferrumequinum
	Alectoris sp.	Rhinolophus birzebburgensis
	Alectoris vel Perdix	Rhinolophus cf. R. euryale
	Perdix nov. sp.	Hystricidae
	Paleocryptonys donnezanii	Hystrix refossa
	Gruidae	Muridae
	Grus grus	Apodemus flavicollis
	Otitidae	Arvicolidae
	Otis tarda	Allophaiomys ruffoi
	Tetrax tetrax	Myodes sp.
	Charadriidae	Gliridae
	Vanellus vanellus	Muscardinus sp.
	Pluvialis apricaria	Leporidae
	Scolopacidae	Hypolagus brachygnatus
	Scolopax rusticola	Oryctolagus etruscus
	Numenius phaeopus vel Numenius	Cercopithecidae
	tenuirostris	Theropithecus sp.
	Tringa totanus	Mustelidae
	<i>Tringa</i> sp.	Mustela cf. M. palerminea
REPTILIA	Philomachus pugnax	Meles meles
Testudinidae	Laridae	Ursidae
Testudo hermanni	Larus canus	Ursus etruscus
Emydidae	Pteroclidae	Canidae
<i>Emys orbicularis</i> group	Pterocles orientalis	Canis mosbachensis
Mauremys sp.	Columbidae	Lycaon lycaonoides
Anguidae	Columba livia	Vulpes cf. V. alopecoides
Pseudopus sp.	Tytonidae	Hyaenidae
acertidae	Tyto aff. T. alba	Pachycrocuta brevirostris
Podarcis sp.	Strigidae	Felidae
Lacerta sp.	Bubo bubo	Lynx issiodorensis
mphisbaenidae	Athene noctua	Megantereon whitei
Blamus sp.	Picidae	Homotherium latidens
Colubridae	Jynx torquilla	Panthera gombaszoegensis
Hierophis viridiflavus	Alaudidae	Acinonyx pardinensis
Zamenis longissimus group	Melanocorypha calandra	Elephantidae
Coronella cf. C. austriaca	Calandrella brachydactyla	Mammuthus m. vestinuss
Natrix natrix	Galerida cristata	Rhinocerotidae
Tiperidae	Alauda arvensis	Stephanorhinus cf. S. etruscus
Vipera aspis group	Motacillidae	Equidae
1	Anthus sp.	Equus altidens
	Turdidae	Equus suessenbornensis
	Turdus sp.	Cervidae
	Sylvidae	Axis eurygonos
	Sylvia cf. S. communis	Praemegaceros obscurus
	Corvidae	Bovidae
	Garrulus glandarius	Bison degiulii
	Pica pica	0
	Pica pica vel Garrulus glandarius	
	Pyrrhocorax graculus vel Corvus monedula	
	Corvus pliocaenus	
	Sturnidae	

Table 1. Faunal list of vertebrates from Pirro Nord Local fauna.

Age (MA), which represents a large temporal interval, characterized by a number of global bioevents.

Such temporal intervals characterized by selected bioevents are almost always integrated and correlated with radiometric dates, magnetostratigraphic data and other possible data allowing their temporal outline.

Faunal Units defined on the basis of presence/absence of taxa, migrations and evolutionary degrees of mammals in a selected area, such as, f.i. the Italian Peninsula, are hardly recognizable in the rest of European regions. Therefore, for a correlation of Italian migration data to the rest of Europe, a geochronological framework as well as a good correlation with marine chronostratigraphy is necessary. On these premises, 17 Faunal Units have been defined (GLIOZZI et al. 1997, PETRONIO & SARDELLA 1999, PETRONIO et al. 2007), representing as many temporal intervals, characterized by faunal assemblages showing different FOs and LOs. Most of these Faunal Units are calibrated with different methods (radiometric dates, magnetostratgraphy etc.) indicating precise time intervals. Pirro F.U., as well as Farneta, Slivia and Melpignano F.Us, constitute an exception, being defined only on biochronological bases (GLIOZZI et al. 1997).



Text-fig. 1. Geographic location of the main localities from the late Early Pleistocene (Farneta to Colle Curti F.U.s) quoted in the text.

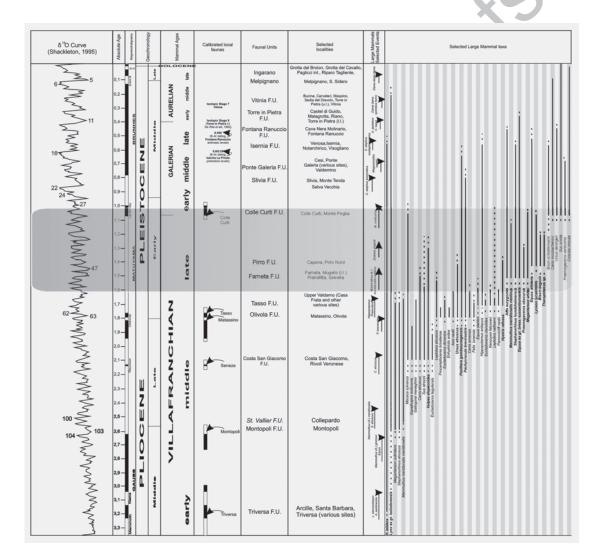
Late Villafranchian: Farneta and Pirro Faunal Units

During the first part of these two temporal phases, an important renewal of faunas is in progress, some species of Villafranchian large mammals progressively disappear while new Middle Pleistocene species gradually arrive. Modifications trophic chains arise, due to the reduction of "green areas" and/or to the gradual onset of different vegetational types, in particular steppes and prairies. Ecosystems are strongly conditioned by quantity and quality of herbivores migrational fluxes, pushed towards southern regions by climatic events. A natural outcome of this situation is a progressive arrival of runner carnivores of different sizes that will gradually replace the older carnivores widespread in the early phases of Pleistocene.

Farneta F.U. is characterized by the presence of Praemegaceros obscurus, a primitive representative of the megacerine group, which will prevail in the later Galerian Mammal Age, replacing the eucladocerines, as well as a large-sized deer belonging to the genus Eucladoceros. Among the middle-sized deers a progress in the local evolution of the genus Axis can be noted: Axis nestii is replaced by a more specialized form (Axis eurygonos), with antlers showing a very short pedicle and a reduced b span, the brow tine is long, very curved and the angle it forms with the beam varies from scarcely obtuse to very open (DI STEFANO & PETRONIO 2002). Among the Bovids, representatives of the genus Leptobos are still present, while among the peryssodactils, the large-sized horse Equus sussenbornensis appears for the first time as well as the brachiodont Stephanorhinus hundsheimensis, whose teeth resemble those of Stephanorhinus etruscus. The smallsized populations appearing in this time period will gradually increase their size during Middle Pleistocene. Mammuthus meridionalis is present with the most specialized subspecies for open spaces: M. m. vestinus. Carnivores keep following the evolutionary trend with ambush hunters (Homotherium latidens) and active hunt typical forms Panthera gombaszoegensis and Pachycrocuta brevirostris, the large hyena that survived up to this time period since the previous F.Us. Megantereon whitei, appears for the first time. This saber-tooth cat has an African origin and its upper canines are much more developed as compared to previous species (SARDELLA 1998).

Our knowledge of Early Biharian (broadly corresponding to the Early Pleistocene) small mammal assemblages assigned to Farneta and Pirro F.Us is limited, and comparisons between faunas testifying different environments are not easy. The arvicolid *Allophaiomys chalinei*, an ibero-occitanic element, is present only in Farneta F.U. (GENTILI et al. 1996, KOT-SAKIS et al. 2003). This species has been reported from many sites of the same age of the Iberian Peninsula (AGUSTI 1992). *Allophaiomys* ex gr. *ruffoi* has been recovered for the first time in the Farneta F.U. (Pietrafitta L.F.), it is rather primitive and has been attributed to an archaic chronomorph of the species *Allophaiomys* ex gr. *ruffoi* Stage A (MARCOLINI et al. in press). Farneta F.U. represents also the last occurrence of *Mimomys pusillus*, an Early Biharian form of small sized *Mimomys*.

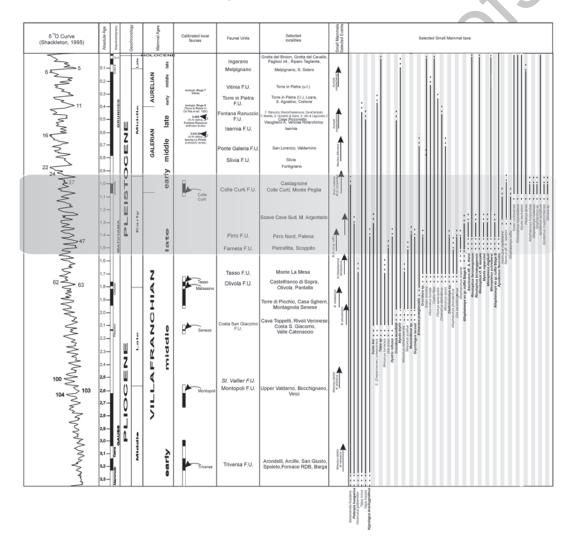
In the following Pirro F.U. the presence of open areas is supported by faunal data. Several large herbivores have been recovered: a primitive bison, *Bison degiulii*, testifying harsher and arid conditions unsuitable for leptobovines; a middle-sized and slender body



Text-fig. 2. Biochronological chart for selected large mammals during Pliocene and Pleistocene in Italy. In bold taxa present in Pirro Nord L.F.

horse, *Equus altidens* has been recovered, while the robust and large-sized horse *E. sussenbornensis* is still present. This F.U. testifies also the FO of some Mustelidae (*Mustela* cf. *M. palerminea* and *Meles meles*), of *Canis mosbachensis*, a canid with lycaon affinities (*Lycaon lycaonoides*), of a cercopithecid of African origin, *Theropithecus* (ROOK et al. 2004, ROOK & MARTIN-EZ-NAVARRO in press), and of a large porcupine, *Hystrix refossa* (ROOK & SARDELLA 2005, ROOK & SARDELLA in press). Both the latter two species are associated with a temperate climate. During this time interval (1.3-1.6 Ma) humans were present in the area of Gargano, as testified by lithic tools recovered in the Pirro Nord deposits, representing therefore, the proof of the oldest European human presence (*Homo georgicus*?) (ARZARELLO et al. 2007, ARZARELLO et al. 2009).

As for small mammals, this F.U. is characterized by the presence of two chronomorphs of the arvicolid *A.* ex gr. *ruffoi*. Indeed, in addition to the primitive form *Allophaiomys* ex gr. *ruffoi* Stage A, present in some of the fissures of the Pirro Nord karstic complex



Text-fig. 3. Biochronological chart for selected small mammals during Pliocene and Pleistocene in Italy. In bold taxa present in Pirro Nord L.F.

and characteristic of the Farneta F.U., the slightly more evolved form *Allophaiomys* ex gr. *ruffoi* Stage B (MAR-COLINI et al. in press) has been described from other Pirro Nord fissures and from Palena (*Allophaiomys* cf. *A. ruffoi*, KOTSAKIS et al. 1992, KOTSAKIS et al. 2003). The evolutionary degree of this taxon is intermediate between that of the type population of the species *A. ruffoi* (Soave Cava Sud, PASA 1947) and that of the populations from the Pietrafitta L.F. and from other Pirro Nord fissures (MARCOLINI et al. in press).

Pirro F.U. is characterized, as far as we know, by the FO in Italy of an extant species of the genus Apodemus (A. flavicollis) and by the LO of Hystrix refossa and of the leporid Oryctolagus lacosti. A diversification of the genus Crocidura (MASINI & SANTINI 1991, FANFANI 2000, KOTSAKIS et al. 2003, SALA & MAS-INI 2007), present with different species in Pirro and Soave Cava Sud L.Fs, is noteworthy. Bats are rather rare in extinct faunas of the Late Villafranchian. They are present only at Pirro Nord (Apulia, Southern Italy) and Ghar Dalam (Malta). At Pirro Nord the FAD of the extant species R. ferrumequinum is reported (Storch 1974, Tata & Kotsakis 2005, Tata & KOTSAKIS in press), while a new species has been described from some fissures of Pirro Nord local fauna. Miniopterus degiulii first described from fissure PN2 and present also in the Sicilian assemblage of Spinagallo Cave (TATA & KOTSAKIS in press) is indicative of a Mediterranean-type environment. The absence of any species of the genus Mimomys is worth to be mentioned here. This genus is widespread in Italy, and in Europe in general, until the end of Early Pleistocene and is present in the assemblages of older F.Us, younger F.Us and in the Soave Cava Sud L.F. (PASA 1947), traditionally correlated with Pirro F.U. (GLIOZZI et al. 1997). The Soave Cava Sud L.F., though, seems to represent a following stage as compared to that represented by Pirro Nord. Indeed at Soave Cava Sud the type population of Allophaiomys ruffoi is present, as well as several species of Mimomys. The L.F. of Monte Argentario (BASCHIERI & SEGRE 1958, SARDELLA 2006, ANGELONE et al. 2008, SARDELLA 2008) where Apodemus flavicollis is also present, can be correlated with the same time interval of Cava Sud, thanks to the presence of Allophaiomys cf. A. ruffoi, showing a comparable evolutionary degree to that of Soave Cava Sud (ANGELONE et al. 2008). The presence and, in some fissures, the predominance of specimens of Apodemus flavicollis over those of Allophaiomys ex gr. ruffoi, as

well as the presence of amphibians and insectivores remains, seems to indicate that the environment was not constantly open during the sedimentation interval of the deposits. Woody areas and humid patches must have been present at some point during the filling of the karstic fissures.

Early Galerian: Colle Curti Faunal Unit

A gradual transition between the typical Villafranchian taxa, most of which are still present in the Pirro F.U., and the modern Galerian assemblages, where Pliocene taxa are lacking, takes place in about 500 ka. During this time interval new steppe/meadowland taxa immigrate in the Italian peninsula from the East or from Central Europe, joining the Villafranchian species, that gradually disappear.

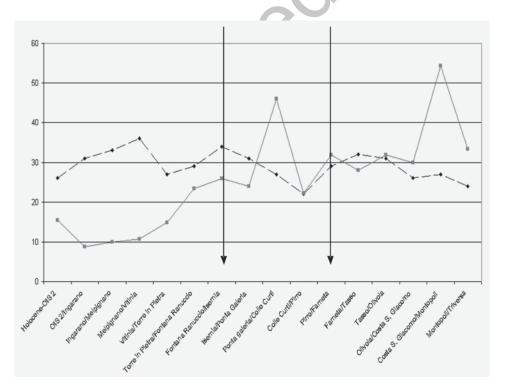
The FO of the large cervid Praemegaceros verticornis in the Colle Curti L.F. (Marche, Central Italy), correlated with the base of Jaramillo Subchron (COL-TORTI et al. 1998), at about 1.1 Ma, is the bioevent that has been chosen to represent the transition between Villafranchian and Galerian (GLIOZZI et al. 1997). This represents a time interval of drastic transformation of the climatic and vegetational cycles, as testified by the marine isotope record and the continental pollen stratigraphy and sometimes referred to as the "mid-Pleistocene revolution" (BERGER & JANS-EN 1994). Cycles become in fact dominated by long glacial periods interrupted by interglacials occurring every 100 ka, i.e., lasting less than the Villafranchian interglacials. The assemblage of Ranica (Lombardia, Northern Italy) testifies to a steppic cold phase, with the presence of the elk Cervalces latifrons (BREDA et al. 2005). Central Italy was dominated by open environments that alternated with woody ones for brief temporal intervals, as testified by pollen diagrams (BERTINI 2000) showing high percentages of erbaceous taxa briefly substituted by forest essences.

As stated above, among large mammals many Villafranchian taxa are still present, such as *Pachycrocuta brevirostris, Panthera gombaszoegensis* and *Homotherium* among Carnivores and *Stephanorhinus* cf. *S. hundsheimensis* (larger sized as compared to the form present in the Farneta F.U.) and *Hippopotamus antiquus* among the Herbivores. The Colle Curti L.F. is not very rich, yet many new elements occur, especially among small mammals (KOTSAKIS et al. 2003, SALA & MASINI 2007). The archaic forms of *Allophaiomys* that characterized the older L.Fs are not present anymore and beginning with this F.U. more evolved forms appear. Indeed SALA & MASINI (2007), differentiate between an Early Biharian I (represented by Farneta and Pirro F.Us) and an Early Biharian II (represented by Colle Curti F.U.). Here Allophaiomys is present either with specimens having simple morphologies and well evolved enamel (Allophaiomys sp., Colle Curti L.F.), and with specimens having a more complex morphology, close to that of Microtus (Microtus): Allophaiomys nutiensis and A. burgondiae (Monte Peglia L.F.). In the context of the above mentioned large mammal faunal renewal, Monte Peglia L.F. testifies also to the FO of many extant taxa, as the murid Apodemus sylvaticus; of the bats Rhinolophus hipposideros and Myotis bechsteini and, among insectivores, of Sorex runtonensis. Among the Pleistocene species the FO of the arvicolid Pliomys lenki is also worth mentioning.

Conclusions

The occurrence of leptobovines and the first occurrence of bisons, that will dominate the Italian peninsula until 550 ka B.P. (Isernia F.U.) thus preventing the dispersal of the genus *Bos* until the Fontana Ranuccio F.U., allows a quite precise biochronological definition of the Pirro Nord large mammal fauna, even though many species have been "inherited" from the previous F.Us. The occurrence of *Equus altidens*, replacing the archaic stenonoid forms, and *Lycaon lycaonoides* that joined the small sized *Canis mosbachensis* are also noteworthy and biochronologically significant. The finding of the primate *Theropithecus* attests to migrations from the African continent, corroborated, though indirectly, by the recovery of Mode1 lithic instruments.

Small mammals represent a transition between the arrival of the first morphologically very simple (i.e. *Allophaiomys pliocaenicus* from Monte La Mesa L.F.) arhizodont arvicolids, and that of the most evolved species of *Allophaiomys (A. nutiensis* and *A. burgondiae* from Colle Curti F.U.), leading towards microtine forms. LOs of *Hystrix refossa, Oryctolagus lacosti* and *Hypolagus brachygnathus* are recorded, while several extant species appear for the first time, as *Apodemus flavicollis* and several bat species. Though radiometric



Text-fig. 4. Turnover rate versus number of taxa for the different F.Us of Plio-Pleistocene in Italy.

dates are lacking at the moment, the presence of *Allophaiomys* ex gr. *ruffoi* and the possibility to define its evolutionary degree allow a biochronological outlining of this fauna. Two evolutionary stages for *Allophaiomys* from these deposits have been recognized: one closer to Farneta F.U. (*Allophaiomys* ex gr. *ruffoi* Stage A from fissures PN34 and PU10) and one slightly more evolved (*Allophaiomys* ex gr. *ruffoi* Stage B from the remaining up to day studied fissures; MARCOLINI et al. in press). Yet these forms are more archaic than that of other Northern Italy deposits (*Allophaiomys ruffoi* type population from Soave Cava Sud).

The chronological time interval of about 500 ka that has been here examined is characterized by a series of climatic cycles that gradually affected not just the flora but also the various large and small mammal communities. In addition to the climatic changes, also paleomagnetic inversions very presumably influenced the bioevents (SARDELLA et al. 1998). Indeed, calculating the number of taxa recovered, not just in the examined time interval but also in the whole Middle Pliocene – Late Pleistocene interval, and comparing it with the Turnover Index (Text-fig. 4), a (approximate) correspondence between the maximum levels of turnovers (line) and the minimum in the values of taxa number (dashed line) is quite evident. This obviously implies that a low faunal renewal rate corresponds to intervals with high biodiversity and viceversa. When comparing the segmented line representing the turnover values with the data representing the paleomagnetic inversion for the Late Villafranchian faunas (Farneta and Pirro F.U.s), the maximum levels of turnovers (line) correspond evidently to the main magnetic variations.

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