

Structural changes in Italian Late Pliocene - Pleistocene large mammal assemblages

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ABSTRACT – A schematic range-chart of the late Pliocene – Pleistocene large mammal genera is presented. The main faunal events recognizable within this time span are discussed. The first faunal event occurs around the Gauss/Matuyama transition with the beginning of the middle Villafranchian characterized by the arrival of *Mammuthus* (Archidiskodon) and *Equus* (the so-called “elephant-Equus event”). The following faunal event occurs at the Plio-Pleistocene transition (the so-called “wolf event”). The latter is marked by a strong contraction in the diversity of the ruminants and by a renewal in the carnivore diversity with the arrival of social carnivores. The low diversity in ruminant assemblage persists until the end of the middle Pleistocene when new arrivals again produce a diversity similar to the final Pliocene one.

RIASSUNTO – [La struttura delle associazioni a mammiferi italiane durante il Pliocene superiore e il Pleistocene] – Viene presentata una carta di distribuzione a livello generico per i grandi mammiferi del tardo Pliocene e Pleistocene dell'Italia e sono discussi i principali eventi faunistici riconoscibili in questo intervallo di tempo. Il primo evento faunistico si verifica in corrispondenza del limite Gauss/Matuyama, con l'inizio del Villafranchiano medio, ed è caratterizzato dall'arrivo di *Mammuthus* (Archidiskodon) ed *Equus* (il cosiddetto “elephant-Equus event”). L'evento faunistico successivo avviene alla transizione Pliocene – Pleistocene (inizio del Villafranchiano superiore). Questo evento è noto come “wolf-event” per l'arrivo in massa di cani di tipo moderno (*Canis etruscus*). Il Villafranchiano superiore è caratterizzato da una forte diminuzione della diversità dei ruminanti e dal rinnovamento dei predatori, con l'arrivo di forme di carnivori sociali. La ridotta diversità dei ruminanti permane per tutto il Villafranchiano superiore sino al Pleistocene medio quando, grazie a nuovi arrivi, si ripristina una diversità comparabile a quella del Pliocene finale.

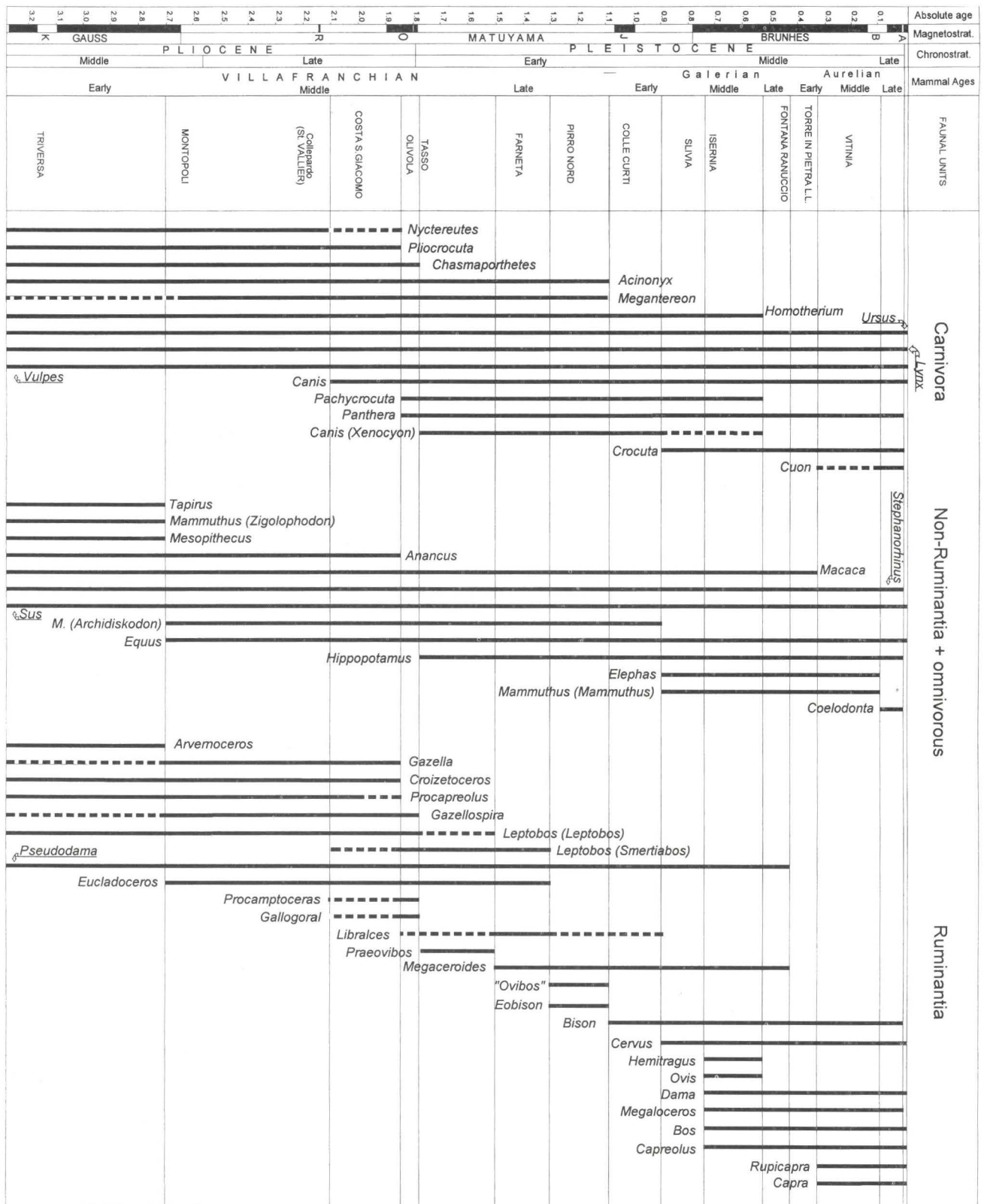
A schematic range-chart depicting the main biologic events spanning the last 3 Ma in Italy is presented and discussed (Text-fig. 1). The chart is a revised summary drawn from Gliozzi *et al.*, 1997 (and references therein), Marchetti (1998) and from Torre *et al.* (1999). The scheme contemplates the genus level, in order to reduce problems in determination and to highlight the most significant environmental signals. The different abundance of remains in the various sites, and consequently the non-homogeneity of the data relative to the different local faunas, surely produces an information bias; it is assumed however that this bias does not significantly affect the general frame of the events. In order to highlight, within the turnover, the changes in structure of mammal communities, we have divided the genera included here into three groups according to a very rough ecomorphology feeding categories, namely: large carnivores, non-ruminant herbivores plus omnivorous and ruminants. Viverrids and mustelids have been excluded from this analysis because of their rarity in the fossil record and therefore the difficulty to place first and last occurrences.

Due to the scanty record of Ruscinian faunas in Italy, not evident here is the dramatic faunal turnover marking the beginning the Villafranchian. The transition from Ruscinian to early Villafranchian faunas is one of major renewal in Plio-Pleistocene mammal

assemblages and is evident in the fossil record of several European countries (cf. Azzaroli *et al.*, 1988; Agustí *et al.*, 1997; Alberdi *et al.*, 1997; Koufos & Kostopoulos, 1997; Radulescu *et al.*, 1997). In Text-fig. 1 at the base of the scheme, are shown the first occurrences of Villafranchian elements together with the older genera that survived this event. The extinctions of previous Ruscinian genera (almost all not occurring in Italy) are intentionally neglected.

The so-called “wolf-event” represents the main faunal turnover in the course of the Villafranchian (Azzaroli, 1985; Rook & Torre, 1996). It occurred at a time lapse included between the Reunion and the end of the Olduvai magnetic intervals (Azzaroli *et al.*, 1988). Other Villafranchian community changes are less well-marked, as for instance that occurring between the end of the Gauss and the beginning of the Matuyama Chrons (the “Elephant-*Equus* event”).

The faunal turnover characterising the “wolf-event” is mainly represented by changes in the ruminant community, which experienced a drastic diversity reduction. On the other hand, non-ruminant herbivores and carnivores display a lower degree of modification, only slight changes in relative species abundance, in which the decline of some forms seems apparently compensated by new occurrences. Among ruminants, the bovids *Gazella*, *Gazellospira*, *Procampoceras* and



Text-fig. 1 - Range chart showing the stratigraphical distribution of ruminant and non-ruminant herbivores and of carnivores. The localities reported with question marks are those of which absolute datings are not available.

Gallagor, and the cervids *Croizetoceros* and *Procapreolus* disappeared, while at the end of the "wolf-event" *Preovibos* made its appearance (Gliozzi *et al.*, 1997). In the course of the Late Villafranchian *Megaceroides* arrived in Italy while *Eobison* and an Ovibovine form made just a fugacious entrance (cf. Masini *et al.*, 1995). Ruminant diversity thus thoroughly changed after the so called "wolf-event", showing a dramatic decrease to low values during the entire Late Villafranchian. In other groups, significant occurrences were those of some carnivores, true *Canis* representatives coming along with the large-sized hyaenid *Pachycrocuta*, with *Panthera* and with the large-sized *Canis* (*Xenocyon*), while other genera vanished, such as *Anancus* among the other herbivores, and *Pliocrocuta*, *Nyctereutes* and perhaps also *Chasmaporthetes* among carnivores. On the whole, extinctions exceeded appearances during the "wolf-event", mostly because of the drastic decline of ruminants.

These mammal turnovers were certainly all induced by the change in climate that modified the vegetation pattern of the area (Bertini, 1994a, b; 1995; Suc *et al.*, 1995a, b). From 5.3 to 4.5 Ma subtropical trees abounded in warm-temperate forests. In southernmost areas, the herbs were especially widespread and the Mediterranean xerophytes were regularly present. From 4.5 to about 3.5–3 Ma in Western Europe and in the North-western Mediterranean areas the subtropical elements declined and a modern vegetation made its appearance. After that time significant thermic differences upset the pre-existing hydric seasonal alternance, inducing the development of the modern Mediterranean vegetation. The instauration of glacial/interglacial cycles from ca 2.6 Ma determines rapid *Artemisia* steppe-deciduous forest alternations at low and mid-altitude in the northwest Mediterranean. Latitudinal differences are responsible for the development of coniferous forest during the glacial cycles in northern Italy and of mixed forest during the interglacials in the southwest Mediterranean region. It is possible that during the early and middle Villafranchian the mosaic vegetation cover developed, thus giving rise to a large number of ecological niches. This structure probably altered during the time spanning the Reunion to end Olduvai magnetic subchron interval, giving rise to a more monotonous environment in which the number of niches considerably reduced. This might explain the severe rearrangements occurring at that time in the mammal communities, especially in ruminants. The appearance of new predators, such as *Canis*, *Panthera*, *Pachycrocuta* and *Xenocyon* increased the predatory pressure which possibly further contributed to the significant reduction in ruminant diversity.

The Villafranchian – Galerian transition is characterised by the lowermost values in mammal richness. This could be in part due to an undersampling of this time interval in Italy, but in any case the trend since the beginning of Late Villafranchian until the

Early Galerian is that of a richness contraction. Mammal richness abruptly increases again in Middle Galerian, reaching a level comparable to that of earliest Late Villafranchian communities.

The environmental changes under the Galerian faunal renewal were probably marked with humid and arid phases, and with periods of probably increased seasonality. During Late Villafranchian some "exotic" essences inherited from the Pliocene flora, as Taxodiaceae, *Liquidambar*, *Carya*, *Pterocarya*, *Eucommia*, *Celtis*, survived but were progressively reduced. The above mentioned genera persist nowadays in south-central Asia and North America, usually in warm-humid regions characterized by low seasonal variations. In the layers just above the mammal bearing level at Colle Curti the last significant occurrence of *Tsuga*, in association with *Cedrus*, is recorded indicating a cool-temperate climate with a high degree of atmospheric humidity (Bertini, 2000; Coltorti *et al.*, 1998). In later times, even during the warmer and wetter phases, the above mentioned "exotic" essences were not reappearing, and it is appropriate to assume that the unsuitable climatic regime and the competition with newly established floral elements definitely displaced such plants. Periods with increased global drought and seasonal variation strongly reduced their range, and made impossible their redistribution.

The mammal and vegetation changes are consistent with the climatic evolution inferred from the $\delta^{18}\text{O}$ curves. The oxygen isotope records of the ODP sites 677 and 846 reported by Shackleton (1995) and Opdyke (1995) show that heavy values begin to increase from the Mammoth magnetic subchron in a steady cooling trend to the end of the Gauss chron. In that time span the cold and warm oscillations were modified from a frequency of about 21ka (orbital precession) to one of about 40 ka (orbital obliquity). This implies considerable variation in the climatic characters and thus in the type and structure of vegetation cover. The next major modification in the isotope record occurs just after the Jaramillo magnetic event, where the 100 ka frequency (orbital eccentricity) is dominant and the amplitude of oscillation increases in agreement with the major glaciations. The beginning of this phase matches the extensive faunal turnover straddling the transition from the Early to the Middle Pleistocene, producing a renewed richness in mammal community.

The faunas analysed here are aggregates derived from what is presumably a variety of environments representing a mixture of community types and ecological settings. Although this fact places some constraints on the interpretation, nonetheless the results emerging provide interesting points.

The striking faunal turnover which signals the beginning of the Villafranchian matches quite sharply the aforementioned 21 to 40 ka change in oscillation frequency of the isotopic curves. At about 2.6 Ma *Equus* and *Mammuthus* (*Archidiskodon*) joined preexisting communities, indicating that marked changes

occurred in the vegetation without any reduction in the number of niches, but on the contrary maybe even with an increase in ecological diversification.

The transition from middle to late Villafranchian, the "wolf-event" does not match any significant oscillation in isotopic curves, but has dramatic consequences in the herbivores' communities structure of Late Villafranchian faunas. It perhaps reflects the re-organisation of the ecologic settings following the previous major events, and, in contrast to the latter, is apparently suggestive of more uniform and ecologically poorer landscapes.

A new major modification oscillation frequency of isotope curves at 100 ka drove the faunal changes linked to the glacial Pleistocene. The middle Galerian is characterized by the dispersals of *Elephas* and *Mammuthus* (*Mammuthus*) and, within ruminants, of *Cervus*, *Dama*, *Megaloceros* and *Capreolus*. *Homo-therium* and *Pachycrocuta*, latest representative of a Villafranchian world, disappear at this time.

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