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LARGE MAMMAL TURNOVER AND DIVERSITY FROM THE PLIOCENE TO THE PLEISTOCENE IN ITALIAN PENINSULA

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Abstract. Patterns of mammalian species turnover, richness, and faunal composition are assessed on the basis of relative sampling quality and correlated with climatic changes. The most important faunal renewals took place at the early to middle Villafranchian, middle to late Villafranchian, and Early to Middle Pleistocene transitions. The turnover phase at Triversa to Montopoli FU transition corresponds to the Middle Pliocene climate worsening, and can be considered a starting point for the dispersal phases that occurred during the Middle and Late Pliocene. Around 1.9-1.7 Ma (Olivola and Tasso FUs) both a clear increase in diversity as well as a turnover pulse can be detected. The so-called "wolf-event" has to be regarded not only as a dispersal phase but also as a true turnover pulse that is related to the climatic changes occurring at the end of the Pliocene. Finally, the transition from Early to Middle Pleistocene faunas represents a major community reorganization (dispersal followed by turnover phase) that shows a significant and progressive rejuvenation coincident with the onset of 100 ka climate cyclicity and vegetation changes related to the climate worsening. The results obtained support the argument that climatic changes are a forcing factor in the first appearances (number of first appearances (Nf) and rate quotient of first appearance (RQf), including migrations) of mammal taxa.

Riassunto. Le faune a grandi mammiferi del Plio-Pleistocene della penisola italiana sono esaminate in termini di ricchezza, diversità e qualità del campione. Le principali fasi di rinnovo, che caratterizzano il passaggio tra le faune del Villafranchiano inferiore e medio, del Villafranchiano medio e superiore e del Galeriano inferiore e medio, vengono analizzate in rapporto ai cambiamenti globali del clima. Il rinnovo faunistico, riconoscibile al passaggio tra le unità faunistiche di Triversa e di Montopoli, può essere visto come l'inizio di una fase di dispersione e diffusione di nuovi taxa nella penisola, che si realizzerà nel corso del Pliocene medio e superiore. Tale evento è da porsi in relazione con il deterioramento climatico globale, che vede l'instaurarsi permanente della calotta glaciale artica ed il predominare della ciclicità con periodo di circa 41 ka. Alla fine del Pliocene, tra circa 1,9, e 1,7 Ma (unità faunistiche di Olivola e Tasso), un nuovo rinnovo determina un sensibile aumento della ricchezza specifica. Il cosiddetto "wolf event" può essere considerato non solo come una fase di dispersione, ma anche come un vero turnover, favorito dalle variazioni climatiche che caratterizzano la fine del Pliocene, in particolare nell'area mediterranea (stadi 64-62 della scala del segnale isotopico dell'ossigeno). La transizione tra faune del Galeriano inferiore e medio, rappresenta la principale riorganizzazione dei complessi faunistici a grandi mammiferi della penisola italiana, caratterizzata da fasi di dispersione, seguite da veri turnover.

Introduction

During the Plio-Pleistocene several important climatic events can be detected that affected faunal and flora richness and turnover. While changes in diversity do not necessarily imply a reconstruction of mammal communities (consistent with the "equilibrium theory' of MacArthur & Wilson 1967), physical and/or biotic environmental variations, principally those caused by climatic changes, can determine concurrent bioevents in multiple lineages. These variations, in turn, can change the community structure as well as affect taxonomic diversity. Some models have been proposed to explain the regulation of faunal diversity with respect to time, emphasising the role played by both physical and/or biotic factors.

Changes in mammal faunal diversity through time has often been considered the result of bioevents correlated with major climatic changes. The role played by environmental factors in diversity changes has been interpreted in various ways.

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Following the "Stationary" model, diversity is primarily regulated by density-dependent factors of the physical environment (Rosenzweig 1975). According to the "Red Queen hypothesis", equilibrium conditions can be maintained by density-dependent extinctions and originations (immigrations), and by coevolution. These changes in equilibrium may be due to internal dynamic of competitive relationships, and do not necessarily predict a close dependence between major climatic changes and evolutionary events (Van Valent 1973; Stenseth & Maynard Smith 1985). Abiotic factors play an important role in diversity changes, as well as, indicated by Vrba (1996 a, b), Behrensmeyer et al. (1997) and Azanza et al. (1999, 2000). With respect to the role played by biotic factor in mammal radiations and extinctions the "Turnover pulse hypothesis" (Vrba 1992, 1996 a) hypothesised that most of lineage turnovers occurred when groups of organism spread in pulses correlated with changes in the physical environment. Accordingly, climatic factors are assumed to be a driving force in diversity changes.

Foley (1994) and White (1996) highlighted some of the problems involved in correlating biotic pulses with climate changes. They maintain that climate affects the evolutionary process primarily through extinctions, whereas the appearance of new taxa depends primarily on factors such as local competitive conditions. Moreover, Alroy (1996) indicated that the apparent correlation between origination and extinction rates is a by-product of statistics, resulting from the need for an artful coincidence of the first and last appearances of taxa known during a single temporal interval.

One of the purposes of this paper is to evaluate the possibility of correlating faunal reconstruction with changes in environmental conditions that were assumed to have occurred at the transition between biochronological units. In order to compare different methodologies, three alternative approaches are tested; two based on unequal (biochronological units) time intervals and one on equal intervals. To evaluate the faunal turnover in unequal intervals, two different methods are used based on the appearances plus extinctions occurring at the same intervals, and on the number of extinctions and new occurrences at the end of a biochron and at the beginning of the successive one (Azanza et al. 1999, 2000; Palombo in press; Torre et al. 1999; and references therein).

This work compares the models resulting from the different methods and evaluates to what extent these models could be considered a statistical artifice, and to what extent do they represent authentic patterns of diversity pulses (or changes in diversity) through time.

Biochronological and environmental framework

The main faunal events occurring during a given time span have been used by various authors (cfr. inter alios Ambrosetti et al. 1972; Azzaroli 1977, 1983; Azzaroli et al. 1988; De Giuli et al. 1983; Caloi & Palombo 1996; Gliozzi et al. 1997; Petronio & Sardella 1999; and references therein) to define a faunal biochronological setting, and to analyse the faunal renewal at the transition between biochronogical units.

Several bioevents related to extinction, origination or local evolution, are considered to be closely related to major pulses of the Neogene-Quaternary glacial trend in the Mediterranean area (Azzaroli 1983; Azzaroli et al. 1988; Caloi & Palombo 1999; Palombo et al. 2003 and references therein; Palombo & Mussi 2001; Sardella et al. 1998; Torre et al. 1999, 2001).

The major event of the latest Miocene (about 6.1 – 5.4 Ma) corresponds with the Messinian salinity crisis (Aguirre et al. 1976; Cita et al. 1995). It has been postulated that this phase provided a number of migration possibilities for land mammals between Africa and Eurasia, although some immigrations may have taken place via Eurasian routes prior to the Messinian crisis (Pickford et al. 1995; Agustí & Llenas 1996). At the Mio-Pliocene transition (around 5.4 Ma) there were significant changes in the physical environment, interpreted as a first pulse of the latest Neogene glacial trends. The turnover pattern offered by Alberdi et al. (1997) for the Mio-Pliocene transition shows a high value of first and last appearances, which seems to be more indicative of a turnover pulse than a dispersal event.

Around 3.3 Ma a cooling phase took place, in which the climate became cooler and drier as documented both in marine and in continental environments (Shackleton 1996). The renewal of mammal assemblages is a global event, evident in the fossil record of Europe as a whole. The Italian faunal complex of the Triversa faunal unit (FU), 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. After Alberdi et al. (1997), the first maximum peaks of diversity in the Mediterranean mammal faunas are detected during the latest Cainozoic time span, at around 3.0 Ma.

The onset of bipolar glaciations occurred between 3.0-2.6 Ma, followed by glacial-interglacial cycles of moderate amplitude sustained at the orbital periodicity of 41 ka (deMenocal & Bloemendal, 1996). In the middle latitude of the North Atlantic the first major influx of ice-rafted debris around the Gauss/Matuyama boundary (oxygen isotopic stage (OIS) 104, Shackleton 1997; Partridge 1997; and reference therein) coincided with a profound change in the Eurasian flora assemblage (i.e. Grichuk 1997). Shackleton (1997, p. 34) points out that the bottom of the Upper Pliocene Gelasian Stage (about 2.5 Ma) approximates the culmination of a series of cycles over which the intensity of the glaciations gradually increases between about 3.0 Ma and about 2.5 Ma. Glacial stages 104, 102 and 100 represent clearly defined events; they are succeeded by less well-defined fluctuations.

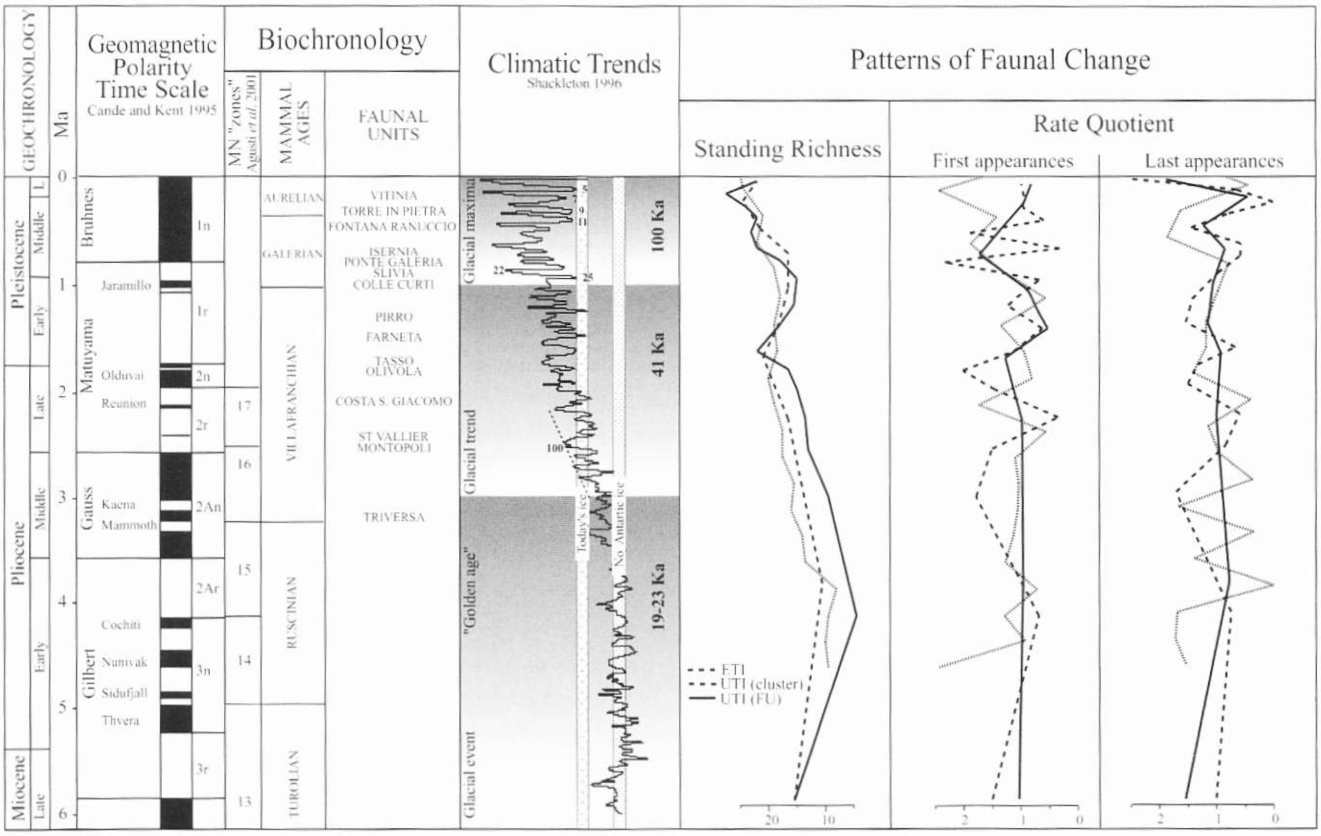

Fig. 1 - Biochronology, diversity and turnover changes of selected large mammal taxa of the Italian Peninsula, dating from the latest Miocene to the Late Pleistocene. Three alternative approaches are considered based on unequal (UTI-BU and UTI-cluster) and equal time (ETI) intervals (see explanations in text). Data from Tab. 1, 2 and 3.

This major biotic event around 2.5 Ma corresponds with the so-called *Equus*-elephant event during the Villafranchian (Steininger et al. 1985; Azzaroli et al. 1988), which has been chosen as the boundary between early and middle Villafranchian (Caloi & Palombo 1996). The profuse changes of flora and fauna during this event have prompted several authors (Alberdi et al 1997; Suc et al. 1997; and the references therein) to propose placing the Plio-Pleistocene boundary here.

Forest taxa markedly diminish in the Italian Montopoli FU, while several new herbivores, large-sized mammals and pachyderms appear. In the north-western Mediterranean area there is also a modification in the vegetation pattern: *Artemisia* steppe is widespread during glacial phases alternating with deciduous forests during interglacial phases (Suc et al. 1995).

After the Middle Pliocene climate worsening, in the time span included between the Reunion normal magnetic episode and the Olduvai magnetochronozone ("Saint Vallier" and Costa San Giacomo FUs, sensu Gliozzi et al. 1997), a slight lowering of the temperature alters the vegetation, at least in the Western Mediterranean area, giving rise to more open environments (Suc et al. 1995; Torre et al. 2001). Among other bioevents, during this time a further faunal renewal can be detected, involving the dispersal of a canid closely related to *Canis etruscus*, the so-called "wolf-event" (Azzaroli 1983). This event is possibly more gradual than previously supposed, culminating at the beginning of Pleistocene at the time of the Tasso FU. During the following Early Pleistocene, there was a slight but progressive decrease in the average temperature. Around 1 Ma a period of cooler and drier conditions, possibly the so-called "Glacial Pleistocene" (Shackleton 1984; Shackleton & Hall 1984) gives rise to a remarkable reconstruction of faunal assemblages and a major community reorganization (see Alberdi et al. 1997). An important faunal reorganization occurred during the climate worsening, which follows the Early/Middle Pleistocene boundary (correlated with OIS 25: Cita & Castradori 1995). Glacial-interglacial phases became more accentuated and the dominant periodicity of variation shifted to 100 ka, corresponding with massive Northern Hemisphere ice sheets (Suc et al. 1995; Shackleton 1996). During the early Middle Pleistocene (middle and late Galerian sensu Gliozzi et al. 1997), phases of climate worsening and periods of increase seasonal variation and aridity favoured a widespread steppe-grass land, while deciduous forests noticeably diminish. Subsequently, from OIS 11, interglacial phases become progressively milder in the Mediterranean area and the average rate of humidity increases (Vergnoux-Grazzini et al. 1990). Broad-leaved wooded areas become more widespread resulting in more fragmented environmental conditions. The beginning of the Last Glacial marked a dramatic change in the vegetation cover that affected both fauna richness as well as structure.

Moreover, it is worth mentioning that due to the complex phisiography of the Italian Peninsula, its remarkable latitudinal extension (in comparison with its longitudinal extension), and the role played by the Mediterranean sea, immigration events were generally more important than emigration events. Hence, the evolution of Italian faunal complexes offer a particularly unique opportunity to analyse the influence of various factors affecting changes in richness, diversity and structure of mammal assemblages through time.

The Italian local faunas, spanning from the Pliocene to the Holocene, have been ordered in a biochronological sequence on the basis of 1) apparence and extinction events, 2) concurrence of taxa, and 3) on the basis of scanty stratigraphic, paleomagnetic and geochronological data. Over time, several biochronological schemes have been proposed that have been eventually divided into Mammal Ages (MAs) and further subdivided into several faunal units (FUs) (Gliozzi al. 1997; Petronio & Sardella 1999) (Fig. 1). Following Alberdi et al. (1997), biochronological units should be assumed to represent "lapses of time during which faunas have certain taxonomic homogeneity, the discontinuity between them corresponding to faunal reconstructions associated with major changes in environmental conditions".

FUs should be considered to be the lowest ranked biochrons, based on multiple bioevents and on all species from local faunas selected as typical associations. Nevertheless, the biochronological scheme currently used for Italian large mammals is based on faunal events that at times are derived from just a few taxa, especially as far as Middle Pleistocene faunas are concerned. Consequently, the FUs proposed for Italian assemblages have only a local value. Nonetheless, these FUs constitute a good tool to test faunal changes from a methodological point of view (Palombo et al. 2003).

Moreover, the scanty Italian faunas belonging to Ruscinian Mammal Age do not permit us to detect the drastic faunal turnover marking the beginning of the Villafranchian MA, which is detectable in the fossil record of several European countries (Agustí et al. 1987; Alberdi et al. 1997; Koufus & Kostopoulos 1997). Accordingly, we have extended our analysis to include the late Turolian faunas in order to highlight, within the turnover, the significance and importance of the changes in diversity and structure of mammal communities at the Miocene-Pliocene transition.

Methodological approaches

An analysis of changes in richness and turnover of Plio-Pleistocene mammal communities from the Italian Peninsula was performed on updated, previously collected data (Azanza et al. 1999; Palombo & Mussi 2001; Palombo et al. 2003). The taxonomical composition of several local faunas has been reconsidered. Both rich assemblages and poorer ones (which also allow biochronological or ecological characterisations) were included. We also selected for analysis taxa that were either commonly found at palaeontological sites, or that had a peculiar biochronological or ecological significance. The biochronological range of the latter taxa was also fully reassessed. In order to evaluate the constraint of these patterns due to biases related to record incompleteness, it was necessary to evaluate the quality of the data.

Data quality

Not all time intervals are equally represented by the same number of species. These differences may reflect actual richness changes or they may be due to incomplete sampling. A standard method for partially correcting the underestimation of richness in a particular interval is to infer the occurrence of known species from preceding and succeeding intervals or of range-through taxa. This method, known as the minimum census technique (Rosenzweig & Taylor 1980), is commonly applied to analyses of mammalian richness (Stucky 1990). The relative sampling quality can be estimated from the proportion of range-through species interval. Two completeness indices (CI) have been proposed: CI ($CI = [N_t / (N_t + N_{rt})] \times 100$) and CIbda ($CI_{bda} = [N_{bda} / (N_{bda} + N_{rt})] \times 100$) (Krause & Maas 1990; Maas & Krause 1994; Maas et al. 1995; see explanations in Azanza et al. 1999). Low index values (< 70, after Maas et al. 1995) are likely to underestimate appearances, disappearances and taxonomic richness of intervals.

Diversity

Diversity is generally used to refer to the number of taxa in a clade or fauna in a given area during a specified interval of time. In this work, we use this definition of diversity to describe the concept of richness. Species richness is commonly measured from the total number of taxa that actually or potentially occur in each interval. This method assumes that all appearances occur at the beginning of the interval and the disappearances at the end. Thus, richness could be overestimated. It is possible to standardise the number of taxa that potentially occur at a given time interval by considering the species richness at the mid point of each time interval (Harper 1975; Maas et al. 1995). This method, called standing richness (Nsr) (Harper 1975), is conceptually similar to the running mean (Webb 1969). Standing richness used as an index of diversity is calculated from the total number of species (Nt), the number of species of every faunal unit (No), the number of species before-during and after every faunal unit (Nbda), and from the number of species before and after but not in a given faunal unit

(Nrt.). Fluctuations of the number of coexisting species could reflect actual richness changes or could be due to incomplete fossil records.

Turnover

A restructuring of the mammal communities could be caused by rapid turnover in which multiple extinctions are followed by a wave of originations. Because speciation and immigration should not be distinguishable, we treat both as 'first historical occurrences' (FO). In like manner, local extinctions are treated as 'last occurrences' (LO). Faunal turnover through time could be assessed simply from the total number of first and last occurrences in each time interval. But this method has inherent biases such as the difference in duration and number of taxa among the time intervals. Rate quotient (RQ) is a method that attempts to normalize these biases. The appearance and disappearence rate quotients (RQf and RQl respectively) are calculated as the ratio: RQ = Ro / Re (Ro = observed number of first or last occurrences; Re = expected number of first or last occurrences). Expected rate is calculated using multiple regressions of the natural logarithm of the observed number of first and last occurrences on the natural logarithm of species richness and the natural logarithm of the duration of the interval (Gingerich 1987). In the case of the ETI (Equal Time Interval) approach it is not necessary to normalize for interval duration. Expected rate is calculated using lest-squared regression of natural logarithm of the observed turnover of first or last occurrences on the natural logarithm of species richness. To assess the overall significance of the observed turnover pattern, we use the chi-square (χ^2) goodness-of-fit to test the departure of the observed pattern from an expected distribution of first and last occurrences (Barry et al. 1995).

Our null hypothesis is that the first and last occurrences should be equally probable in all intervals and consequently, should be randomly distributed among the intervals. In other words, appearances and disappearances can occur at any moment. The alternative hypothesis is the pattern observed: first and last occurrences are concentrated in certain moments that are not due to chance but rather to concrete causes - global changes.

An alternative approach is the bootstrapping method formulated by Gilinsky (1991) and modified by Maas et al. (1995). This method tests the null hypothesis that first and last occurrences are randomly distributed among faunal intervals. The test distribution of each interval consists of the expected numbers of first and last occurrences generated for each of 10,000 simulations. For each simulation, species ranges are shuffled randomly among intervals taking into account that each species has only one appearence event and one disappearence event, datum, and ranges cannot be truncated.

A major problem in explaining the regulation and maintenance of diversity using the fossil record is how to control variations through time.

In this paper, three alternative approaches are considered based on unequal time intervals (biochronological units) (UTI-BU and UTI-cluster approaches), equal time intervals (ETI approach), and turnover index (TI approach). For this latter approach, appearances and disappearances of taxa at the transition between each biochronological unit were counted.

The unequal time intervals (UTI) approach

The unequal times intervals used first are the BUs (MAs for the Late Miocene and Earliest Pliocene faunas, FUs for the more recent ones), whose possible duration varies from 1 Ma to 100 ka (UTI-BU). This length of duration is especially true for the Middle Pleistocene FUs, which conveniently match, more or less, the Middle Pleistocene interglacial/glacial cycles.

A second analysis is performed using the cluster resulting from a multivariate method based on the common presence of taxa, previously applied to test the affinity among selected Italian local faunas (LFAs) from the latest Miocene to late the Middle Pleistocene (Palombo et al. 2003) (UTI-cluster).

The relative sampling quality among these unequal intervals is estimated by completeness indices (CI and CIbda; Maas et al. 1995) based on the proportion of range-through taxa and inferred occurrences of taxa lacking in a given FU, but known from preceding and succeeding ones.

The equal time intervals (ETI) approach

An alternative approach is to use equal intervals, but this requires precise ordering of the first and last appearance events of taxa. This ordering cannot be achieved directly from the Plio-Pleistocene continental record of the Italian Peninsula because most of data come from isolated localities and age calibrations are very scarce. The parsimony-based methods developed by Alroy (1992) are used to establish the appearance event sequence. Chronological relationships are detected that identify the taxa that have an overlapping (conjunct) or non-overlapping (disjunctive) distribution across sets of taxonomic lists (Alroy 1992, 1994). Calibration of the appearance event sequence is possible from the available radio-isotopic and paleomagnetic data of selected localities (Alroy 1992). Nevertheless, this calibration introduces a temporal distortion that becomes greater as available dating diminishes, such as in the case of Italian faunas. In our case (Fig. 2), the distortion between actual and estimated ages of localities indicates a contraction of time between 4.5 and 2.5 Ma (Turolian – Ruscinian – early middle Villafranchian), and quite good correspondence during the time span from 2.0 to 400 ka (late Villafranchian-late Galerian). The early and middle Aurelian are placed more recently, between 400 and 0 ka. To define an optimal interval length, the order of magnitude corresponding to the minor length

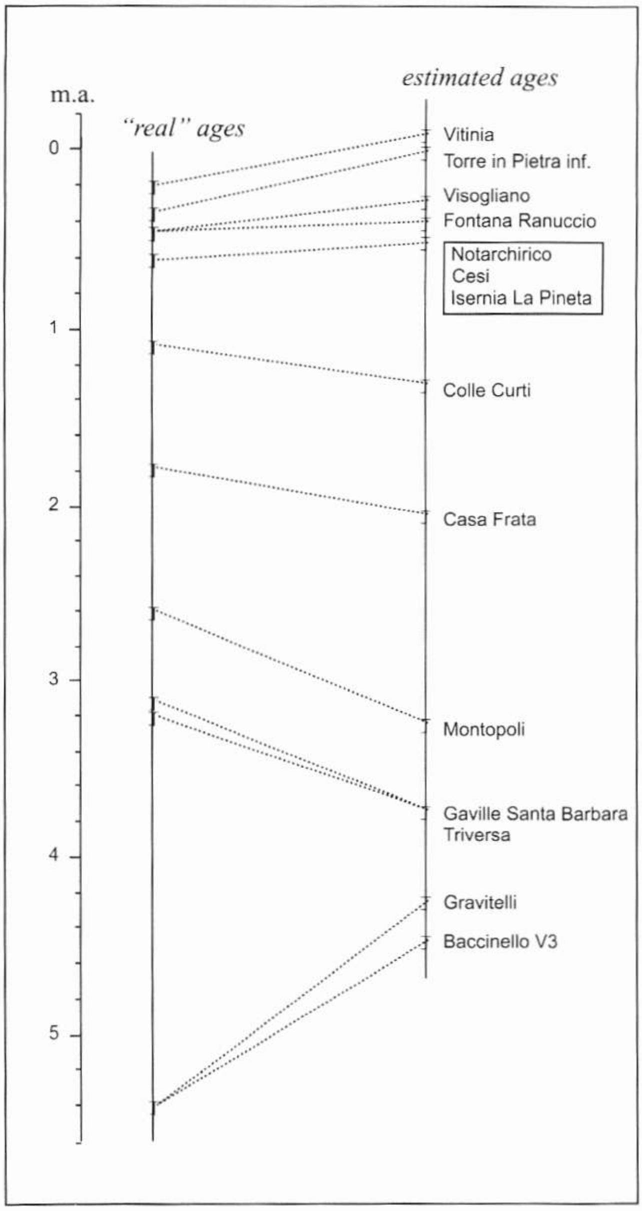

Fig. 2 - Calibration of the appearance event sequence is possible from radio-isotopic and paleomagnetic ages estimated for localities (Alroy 1992, 1994; Azanza et al. 1999). Nevertheless, this calibration introduces a temporal distortion that becomes increasingly greater as available dating is less. The distortion between "real" and "estimated" age of Italian selected localities are here expressed graphically.

of the biochronological units (0.25 Ma) is selected, so as not to eclipse evolutionary events. Completeness indices are not calculated in the equal time approach.

The turnover (TI) approach

Diversity in taxonomical composition between two succeeding biochrons can be regarded as a faunal turnover when the renewal is due both to local extinctions and to appearances of taxa. An increase or decrease of richness depending on only one of these factors has to be regarded as a dispersal or extinction event.

Consequently, faunal renewals can also be estimated from the number of extinctions and appearences at the end of a biochron and at the beginning of the successive one. As previously, both speciation and immigrations can be treated as 'first occurrences', and local extinctions as 'last occurrences'. This method of analysis enables us to test if some niches that became available during a given FU will be occupied by new immigrants during the succeeding interval. The ecological preferences of extinct and new comers taxa also allow us to evaluate changes in the structure of mammal communities (Palombo & Mussi 2001).

Turnover indices ($TI = \% FO + \% LO / 2$) are calculated using first occurrence ($\% FO = FO / RM \times 100$) and last occurrence ($\% LO = LO / RM \times 100$) percentages. This permits us to normalise LO and FO from the number of species (N) at the transition between two successive biochronological units using a running mean ($RM = N - (FO + LO / 2)$ as in Torre et al. (1999).

Results

The Italian large mammal complexes have changed through time in composition, richness and structure. These variations have been determined by concurrent events such as dispersal phases and extintion events. As discussed above, fluctuation of coexisting species numbers may reflect actual richness changes or may be due to incomplete sampling. The value of the mammalian species completeness index CI resulting from the UTI-BU analysis is consistently high throughout the entire time span considered. The lowest values of Saint Vallier, "Ponte Galeria" (CI=67) and Fontana Ranuccio (CI=71) are very close to the minimum values indicated for a correct estimation of appearances, disappearances and taxonomic richness (< 70, Maas et al. 1995) (Fig. 3). The more conservative CIbda index shows significantly lower values with respect to Saint Vallier and "Ponte Galeria" FUs. This would be expected considering the high number of range-through species and the low proportion of species present before, during and after these intervals. Consequently, the richness of the above mentioned FUs could be underestimated, as could be to a lesser degree, the standing richness of late Villafranchian and Galerian FUs (from Farneta to Slivia). The results of the UTI-cluster analysis provide quite similar results. The CI index shows high values for all intervals, whereas the values of CIbda index reach their minimums in the intervals corresponding to latest Villafranchian, early Galerian and "Ponte Galeria" clusters.

The largest numbers of taxa occur at Tasso, Isernia and "Vitinia" FUs. The highest values of completeness (CI and CIbda) were also recorded in these FUs, as well as in the Triversa FU (Fig. 3 and 4).

Standing richness

The standing richness shows similar patterns in both

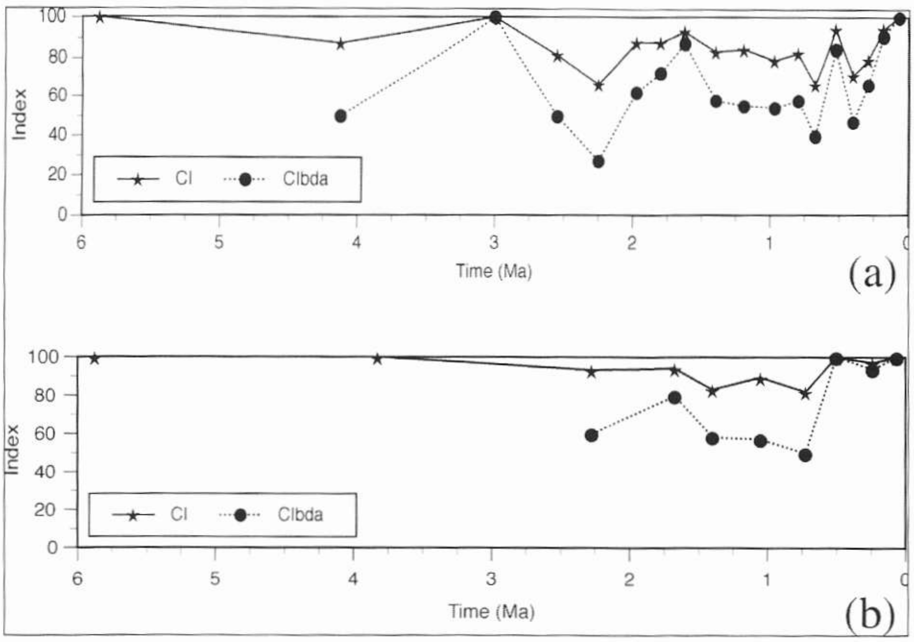

Fig. 3 - Mammalian species completeness indices per interval plotted against time interval, using the UTI- BU (a) and UTI-cluster (b) approaches.

the UTI and ETI approaches (Fig. 1; Tab. 1, 2 and 3). UTI analysis reveals that the standing richness measured on the basis of species occurrences in biochronological units generally increases from the Ruscinian MA to the Plio-Pleistocene. Two major fluctuations can be detected that correspond to the very important flexion at the end of the Turolian and to a less important flexion during the late Villafranchian. Both fluctuations are followed by an increase in the number of species. This increase is more gradual during early and middle Villafranchian MAs. The richness minimum value corresponds to Ruscinian, which is in agreement with the scanty knowledge of Italian local faunas belonging to this MA. Consequently, extinction value at the end of Turolian was overestimated.

During the early and middle Villafranchian, new ap-

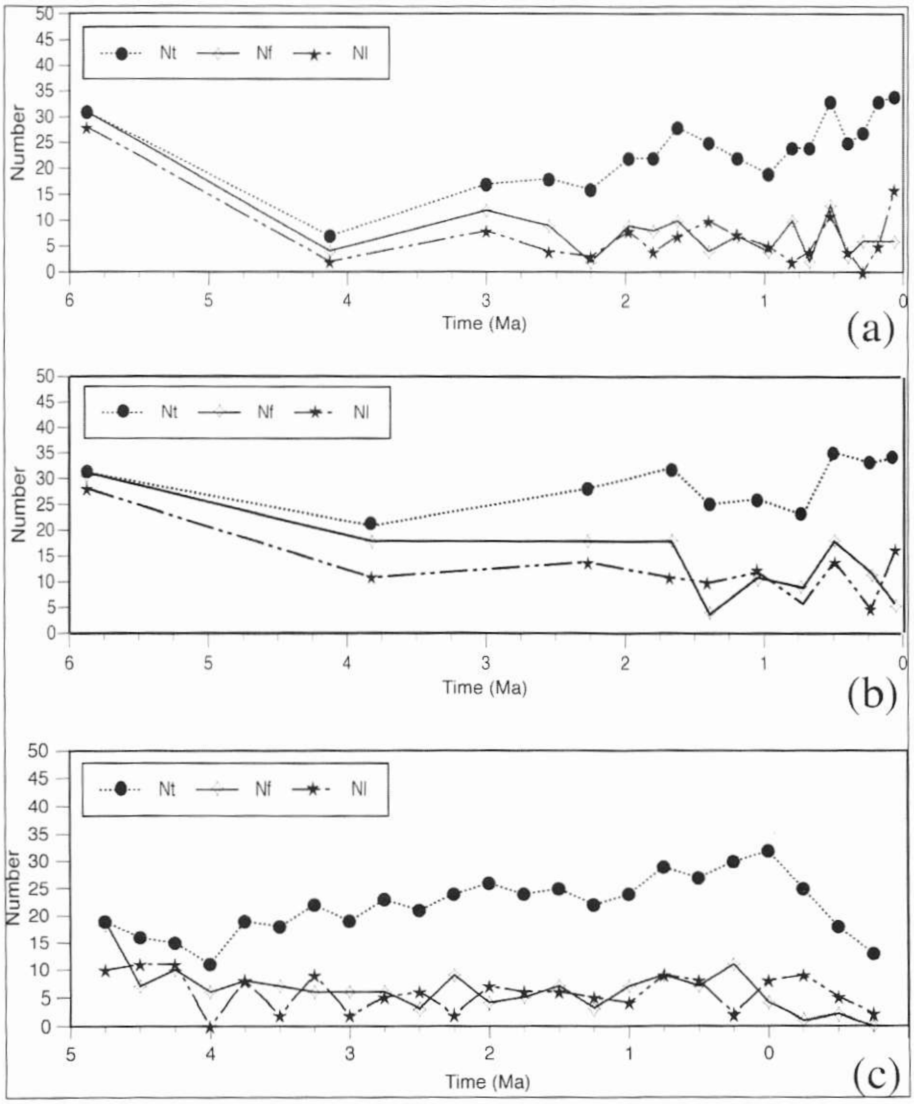

Fig. 4 - Maximum number of species (Nt) and the first- and last occurrences per interval plotted against time interval, using the UTI- BU (a) and UTI-cluster (b) and ETI (c) approaches.

									First occurrences					Last occurrences				
FU	Span (Ma)	Nt	Nrt	No	Nbda	CI	CIbda	Nsr	Obs.	Exp.	χ^2	RQ		Obs.	Exp.	χ^2	RQ	
Turolian (MN13)	1.85	31	0	28	0	100		15.5	31	20.58	5.27	1.51		28	28.09	0.00	1.00	(+++)
Ruscinian (MN14+15)	1.65	7	1	1	1	88	50	4.5	4	5.95	0.64	0.67	(+)	2	2.72	0.19	0.74	
Triversa	0.6	17	0	5	2	100	100	9.5	12	6.69	4.22	1.79	(++)	8	4.69	2.34	1.71	
Montopoli	0.3	18	4	3	4	82	50	13	9	6.00	1.50	1.50		4	4.75	0.12	0.84	
Saint Vallier	0.3	16	8	0	3	67	27	13.5	2	6.22	2.86	0.32	(-)	3	5.09	0.86	0.59	
Costa San Giacomo	0.25	22	3	3	5	88	63	15	9	6.18	1.29	1.46		8	5.33	1.34	1.50	
Olivola	0.1	22	3	1	8	88	73	16.5	8	3.95	4.15	2.02		4	3.04	0.34	1.32	(-)
Tasso	0.25	28	2	5	14	93	88	22	10	8.88	0.14	1.13		7	10.67	1.26	0.66	
Farneta	0.2	25	5	1	7	83	58	18.5	4	6.61	1.03	0.60	(-)	10	6.52	1.86	1.53	
Pirro	0.21	22	4	1	5	85	56	15.5	7	5.75	0.27	1.22		7	4.92	0.88	1.42	
Colle Curti	0.24	19	5	1	6	79	55	15	4	6.03	0.68	0.66		5	5.16	0.00	0.97	
Slivia	0.1	24	5	0	7	83	58	18	10	4.29	7.59	2.33		2	3.56	0.68	0.56	(-)
Ponte Galeria	0.15	24	12	2	8	67	40	22	2	6.58	3.19	0.30	(--)	4	7.09	1.35	0.56	
Isernia	0.15	33	2	4	11	94	85	23	13	6.87	5.47	1.89		11	7.69	1.43	1.43	
Fontana Ranuccio	0.1	25	10	1	9	71	47	22	3	5.19	0.93	0.58	(-)	4	5.12	0.25	0.78	(-)
Torre in Pietra	0.12	27	7	0	14	79	67	24	6	6.27	0.01	0.96		0	6.94	6.94	0.00	(---)
Vitinia	0.1	33	2	0	20	94	91	27.5	6	6.42	0.03	0.94	(-)	5	7.68	0.94	0.66	(-)
Late Aurelian	0.13	34	0	2	12	100	100	22	6	6.05	0.00	0.99		16	6.32	14.82	2.53	
										Chi-square 39.285					Chi-square 35.567			
										Sig. Level 0.0016					Sig. Level 0.0052			

Tab. 1 - Mammal species turnover and richness for the unequal time intervals (Turolian and Ruscinian mammal ages and Villafranchian, Galerian and Aurelian faunal units, after Gliozzi et al. 1997 and Petronio & Sardella 1999) from the latest Miocene to Recent in the Italian peninsula. $\mathbf{N}_t$: number total of species, $\mathbf{N}_{rt}$: number of species range through time; $\mathbf{N}_o$: number of species known only; $\mathbf{N}_{bda}$: number of species recorded before, during, and after an interval; **CI**, $\mathbf{CI}_{bda}$: completeness indices; and $\mathbf{N}_{sr}$: standing richness. Obs.: observed, Exp.: expected. Expected appearances were calculated as: Re = exp [0.063 + 0.949 ln(Nsr) + 0.586 ln(duration)] and expected disappearences were calculated as: Re = exp [- 2.132+ 1.815ln(Nsr) + 0.801 ln(duration)]. RQ: Rate Quotient, overall significance of the observed turnover pattern by chi-square goodness-of-fit and χ^2 values are also given for each interval. Significantly high observed turnover is indicated by "+" and significantly low observed turnover is indicated by "-" based on comparison with bootstrapped distribution. (+ + +) or (- - -) at $p< 0.001$, (+ +) or (- -) at $p< 0.01$, and (+) or (-) at $p< 0.05$.

pearences outnumber extinctions and the number of species progressively increases. At the end of Pliocene and beginning of late Villafranchian, the standing richness at the Olivola FU reaches a value comparable to that of the Turolian MA. This progressive faunal renewal seems to eventually be completed at Tasso FU (late Villafranchian) where a notable peak in the standing richness value can be detected.

The same increase in richness characterises the Olivola+Tasso interval in the UTI cluster analysis, whereas in the ETI analysis the highest richness value of the Plio- Early Pleistocene corresponds to the time lapse between about 2.0-1.75 Ma, which is more or less equivalent to the beginning of late Villafranchian.

During the following Early Pleistocene (Farneta, Pirro and Colle Curti FUs), UTI-BU analysis reveals

									First occurrences					Last occurrences				
	Span (Ma)	Nt	Nrt	No	Nbda	CI	CIbda	Nsr	Obs.	Exp.	χ^2	RQ		Obs.	Exp.	χ^2	RQ	
A1 Turolian	1.85	31	0	28	0	100		15.5	31	29.78	0.05	1.04		28	18.27	5.18	1.53	(+++)
A2 Ruscinian + Triversa	2.25	21	0	8	0	100		10.5	18	18.79	0.03	0.96	(++)	11	14.64	0.91	0.75	
B111 Middle Villafranchian	0.85	28	2	9	3	93	60	16.5	18	18.59	0.02	0.97		14	14.18	0.00	0.99	
B112 "a" Olivola + Tasso	0.35	32	2	7	8	94	80	21	18	14.12	1.07	1.27		11	12.09	0.10	0.91	
B112 "b" Farneta	0.2	25	5	1	7	83	58	18.5	4	7.71	1.78	0.52	(--)	10	8.84	0.15	1.13	
B12 Pirro + Colle Curti	0.5	26	3	4	4	90	57	16.5	11	12.61	0.21	0.87		12	11.55	0.02	1.04	
B21 Ponte Galeria (+ Venosa)	0.15	23	5	2	5	82	50	16.5	9	5.23	2.72	1.72		6	7.25	0.22	0.83	(--)
B221 Slivia + Isernia + FontanaR	0.3	35	0	5	8	100	100	21.5	18	13.08	1.85	1.38		14	11.60	0.50	1.21	
B222 early-middle Aurelian	0.22	33	1	0	15	97	94	24.5	12	12.77	0.05	0.94		5	11.37	3.57	0.44	(---)
Late Aurelian	0.13	34	0	2	12	100	100	22	6	7.36	0.25	0.82	(--)	16	8.54	6.51	1.87	
										Chi-square 8.017					Chi-square 17.048			
										Sig. Level 0.5324					Sig. Level 0.0465			

Tab. 2 - Species turnover and richness for the 10 unequal time intervals (cluster) as obtained for Italian mammal faunas from the latest Miocene to Recent (Palombo et al. 2003). $\mathbf{N}_t$: number total of species, $\mathbf{N}_{rt}$: number of species range through time; $\mathbf{N}_o$: number of species known only; $\mathbf{N}_{bda}$: number of species recorded before, during, and after an interval; **CI**, $\mathbf{CI}_{bda}$: completeness indices; and $\mathbf{N}_{sr}$: standing richness. Obs.: observed, Exp.: expected. Expected appearances were calculated as: Re = exp [- 1.304 + 1.55 ln (Nsr) + 0.731 ln (duration)] and expected disappearances were calculated as: Re = exp [0.576 + 0.763 ln (Nsr) + 0.387 ln (duration)]. RQ: Rate Quotient, overall significance of the observed turnover pattern by chi-square goodness-of-fit and χ^2 values are also given for each interval. Significantly high observed turnover is indicated by "+" and significantly low observed turnover is indicated by "-" based on comparison with bootstrapped distribution. (+ + +) or (- - -) at $p< 0.001$, (+ +) or (- -) at $p< 0.01$, and (+) or (-) at $p< 0.05$.

					First appearances					Last appearances				
	Nt	No	Nbda	Nsr	Obs.	Exp.	$\chi 2$	RQf		Obs.	Exp.	$\chi 2$	RQl	
4.75-4.5	19	10	0	9.5	19	7.76	16.30	2.45		10	6.53	1.84	1.53	(+)
4.5-4.25	16	6	4	10	7	7.53	0.04	0.93		11	6.42	3.28	1.71	(++)
4.25-4.0	15	8	3	9.5	10	7.76	0.65	1.29	(++)	11	6.53	3.05	1.68	(++)
3.0-3.75	11	0	5	8	6	8.57	0.77	0.70	(+)	0	6.95	6.95	0.00	(--)
3.75-3.5	19	5	8	13.5	8	6.33	0.44	1.26		8	5.76	0.87	1.39	
3.5-3.25	18	1	10	14	7	6.20	0.10	1.13		2	5.69	2.39	0.35	(-)
3.25-2.0	22	3	10	16	6	5.74	0.01	1.05		9	5.42	2.36	1.66	
3.0-2.75	19	1	12	15.5	6	5.84	0.00	1.03		2	5.48	2.21	0.36	(-)
2.75-2.5	23	0	12	17.5	6	5.45	0.06	1.10		5	5.25	0.01	0.95	
2.5-2.25	21	2	14	17.5	3	5.45	1.10	0.55		6	5.25	0.11	1.14	
2.25-2.0	24	1	14	19	9	5.19	2.79	1.73		2	5.10	1.88	0.39	(-)
2.0-1.75	26	1	15	20	4	5.04	0.21	0.79		7	5.01	0.79	1.40	
1.75-1.5	24	0	13	18.5	5	5.27	0.01	0.95		6	5.15	0.14	1.17	
1.5-1.25	25	1	13	19	7	5.19	0.63	1.35		6	5.10	0.16	1.18	
1.25-1.0	22	0	14	18	3	5.36	1.04	0.56	(-)	5	5.20	0.01	0.96	
1.0-0.75	24	1	14	19	7	5.19	0.63	1.35		4	5.10	0.24	0.78	
0.75-0.5	29	4	15	22	9	4.77	3.75	1.89		9	4.84	3.58	1.86	
0.5-0.25	27	3	15	21	7	4.90	0.90	1.43		8	4.92	1.93	1.63	
0.25-0.0	30	2	19	24.5	11	4.48	9.48	2.45		2	4.65	1.51	0.43	(--)
0.0-+0.25	32	1	20	25.5	4	4.38	0.03	0.91	(-)	8	4.59	2.54	1.74	
+0.25- +0.5	25	1	16	20.5	1	4.97	3.17	0.20	(--)	9	4.96	3.29	1.81	
+0.5- +0.75	18	0	11	14.5	2	6.07	2.73	0.33	(-)	5	5.62	0.07	0.89	
+0.75-present	13	0	11	12	0	6.77	6.77	0.00	(--)	2	6.01	2.68	0.33	
						Chi-square 51.63					Chi-square 41.89			
						Sig. Level 0.0004					Sig. Level 0.0065			

Tab. 3 - Mammal species turnover and richness for the 23 equal time intervals in the last 5.5 Ma. N_t: number of species; N_o: number of species known only; N_{bda}: number of species recorded before, during, and after an interval; N_{sr}: standing richness. Obs.: observed, Exp.: expected. Expected appearances were calculated as: Re = exp [-0.579 ln(Nsr) + 3.352] and disappearances were calculated as: Re = exp [-0.358 ln(Nsr) + 2.683]. RQ: Rate Quotient, overall significance of the observed turnover pattern by chi-square goodness-of-fit and χ^2 values are also given for each interval. Significantly high observed turnover is indicated by "+" and significantly low observed turnover is indicated by "-" based on comparison with bootstrapped distribution. (+ + +) or (- - -) at $p< 0.001$, (+ +) or (- -) at $p< 0.01$, and (+) or (-) at $p< 0.05$.

that richness decreased, attaining values similar to those of the end of the middle Villafranchian (Costa San Giacomo FU). UTI-cluster and ETI analyses produce similar richness patterns, although decrease in richness in the latter is less evident.

The Middle Pleistocene is characterised by the highest standing richness values that progressively increase from Slivia to "Vitinia" FU (but see addenda). The richness value does not show any important pulses, except at the Fontana Ranuccio FU, where a slight flexion can be detected (possibly related to the low value of CIbda index) (Fig. 3). In effect, UTI-cluster analysis shows that a progressive increase in richness occurs from Slivia FU to "Vitinia" FU without any fluctuation. These results are consistent with the data obtained from the equal time interval analysis.

Turnover

Turnover changes can be estimated as rate quotients that normalize the number of first and last occurrences in the intervals taking into consideration both the duration and the differences in species richness among them, calculated as the ratio of observed to expected turnover (Gingerich 1987). Using this methodological approach it is possible to exam the faunal renewal during the time corresponding to a biochronological unit, and to highlight the differences in taxonomical composition between successive biochrons.

The results of the analysis (Fig. 1) based on FUs (unequal time interval) first and last appearance rate quotients (RQf and RQl respectively) match each other quite closely during the last Miocene to early Pliocene time, suggesting that the rate of appearences and diasappearences may compensate each other and that a broad range of rates might be possible within this "equilibrium". At the transition from Turolian to Ruscinian MAs, appearences surpass disappearances in quotient, but not in total number. Notwithstanding, the lowest standing richness value is observed at Ruscinian. The relative quotient between first and last occurrences shows a similar trend between the Ruscinian MA and the Triversa FU and between

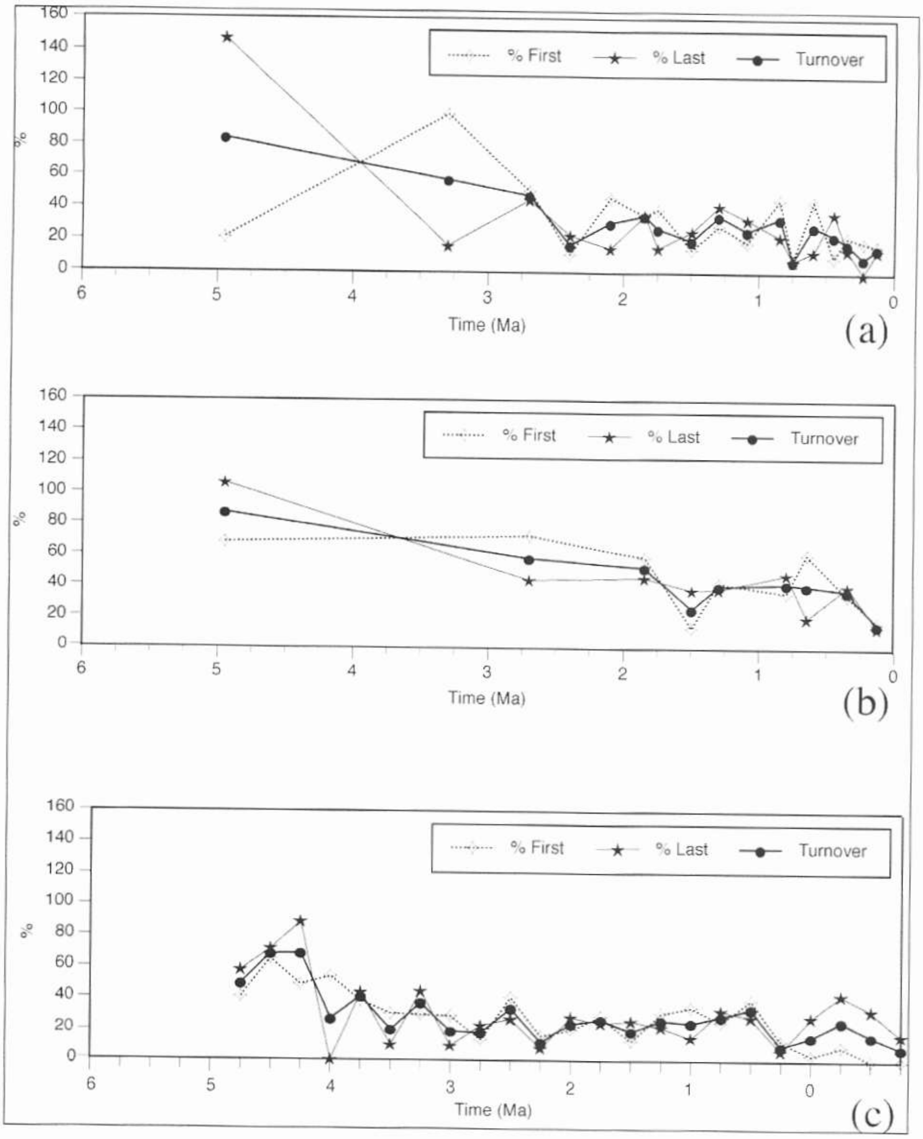

Fig. 5 - Last (%LO) and first (%FO) occurrences percentages, and turnover indices plotted against time interval, using the UTI- BU (a) and UTI-cluster (b) and ETI (c) approaches.

the Saint Vallier and Isernia FUs. Particularly similar in pattern are the rate quotients from "Ponte Galeria" to Isernia FUs. Moreover, the high values of both RQf and RQl corroborate the turnover pulses that occurred at the Triversa, Costa San Giacomo and Isernia FUs. The main differences in rate quotients (RQf and RQl) can be detected during both the early Villafranchian (Triversa FU) and early middle Villafranchian (Montopoli FU), when appearences tend to prevail, and during the early late Villafranchian (Olivola + Tasso FUs). The RQf reaches its maximum value at the beginning of the middle Galerian (Slivia FU) when first occurrences clearly dominate. RQf reaches its maximum value at the beginning of the middle Galerian (Slivia FU) when first occurrences outnumber last occurrences. During the Isernia FU first and last occurrences are quite important both in rate quotient and in total number of species involved. Minor changes characterise the late Galerian and Aurelian MA, during which time the RQf does not vary significantly. The highest value of standing richness is detected at the "Vitinia" FU, while the RQl remains unchanged.

Turnover analysis based on UTI-cluster emphasises the prevalence of RQf during the early late Villafanchian and even more markedly during the middle Galerian. The maximum value of RQl occurs at the transition from Galerian to Aurelian MA.

Equal time interval analysis (ETI) generates rate quotients that tend to be more inhomogeneous than those resulting from UTI analyses. Nevertheless, the results of equal time interval analysis are consistent with the other methodological approaches with respect to the global trend of RQf, especially as far as late Villafranchian and Galerian is concerned. Some minor differences can be detected in the trend of RQl , primarily in the late Galerian and Aurelian.

Finally, the comparatively high values of both RQf and RQ1 obtained from both the ETI and UTI (BU and cluster) analyses confirm the turnover pulses at Triversa, Costa San Giacomo, Pirro and Isernia FUs. Considering the results as a whole, the major turnover pulse seems to have taken place during the beginning of the Galerian MA.

The results obtained from ETI, UTI-BU, UTI-cluster, and bootstrapping analyses are all very similar. As mentioned previously, we used the chi-square goodness-to-fit to test the observed turnover pattern. First and last occurrences are significantly heterogeneous among intervals using the equal time interval approach ($\chi^2 = 51.63$ for first occurrences and $\chi^2 = 41.89$ for last occurrences; $p < 0.01$ and $p < 0.1$ respectively, and degree freedom = 22). First and last occurrences are also significantly heterogeneous in both the unequal faunal units time interval ($\chi^2 = 39.29$ for first occurrences and $\chi^2 = 35.57$ for last occurrences; $p < 0.1$ and degree freedom = 17) and the unequal cluster

INTER	NCYC	Mδ^{18}O	mδ^{18}O	MODAL	CLIMVAR	MAGCAM	Nsr	RQf	RQl
0,0-0,25	4	4,14	0,55	3,399	3,59	0,385	12	0,00	0,33
0,25-0,5	3	3,87	0,84	3,014	3,03	0,154	14,5	0,33	0,89
0,5-0,75	5	3,29	1,27	2,86	2,02	0,892	20,5	0,20	1,81
0,75-1,0	4	3,57	1,4	1,968	2,17	0,232	25,5	0,91	1,74
1,0-1,25	5	2,91	1,4	2,2	1,51	0,062	24,5	2,45	0,43
1,25-1,5	7	2,81	1,47	2,262	1,34	0,607	21	1,43	1,63
1,5-1,75	5	2,86	1,22	1,655	1,64	0,43	22	1,89	1,86
1,75-2,0	2	2,41	1,35	2,085	1,06	0,195	19	1,35	0,78
2,0-2,25	4	2,62	-0,6	1,89	3,28	0,935	18	0,56	0,96
2,25-2,5	4	2,43	0,78	0,955	1,75	0,275	19	1,35	1,18
2,5-2,75	3	1,56	0,49	0,685	1,07	0,51	18,5	0,95	1,17
2,75-0,3	2	1,54	0,84	1,195	0,7	0,685	20	0,79	1,40
3,0-3,25	3	1,29	0,12	0,51	1,17	0,19	19	1,73	0,39
3,25-3,5	2	1,55	-0,25	0,7	1,8		17,5	0,55	1,14

a

	MCC	MCV	Max. δ^{18}O	Min. δ^{18}O	MODE	NCY
MCC	1					
MCV	0.044	1				
Max. δ^{18}O	-0.154	0.719**	1			
Min. δ^{18}O	-0.207	-0.218	0.423	1		
MODE	-0.071	0.495	0.851**	0.518	1	
NCY	0.198	0.309	0.568*	0.489	0.437	1

b

	Nsr	RQf	RQl
Number of cycles			
Max. δ^{18}O			
Min. δ^{18}O	0,750**		
Mode δ^{18}O			
Climatic variation		0.601*	
Magnitude of change			

* = $p < 0.05$; ** = $p < 0.01$

c

Tab. 4 - 4a: Matrix of the climatic data for the last 3.5 Ma in relationship with ETI intervals. 4b: Correlation coefficients between climatic variables for the 3.5 Ma dataset. 4c: Significant correlation coefficients between faunal events and 3.5 Ma climatic variables (all species). * = $p < 0.05$ and ** = $p < 0.01$. Abbreviations: INTER: equal intervals; NCY: numbers of cycles; Mode: temperature modal; MCV: magnitude of climatic variations; MCC: magnitude of climatic changes; Nsr: standing richness; RQf: appearence rate quotient; RQl: disappearence rate quotient.

time interval ($\chi^2 = 8.02$ for first occurrences and $\chi^2 = 17.05$ for last occurrences; $p = 0.01$ and $p < 0.5$ respectively, and degree freedom = 9). As a result, we reject the null hypothesis for all three approaches. For each interval, the observed numbers of first and last occurrences are compared with the expected numbers generated for each of the 10.000 simulations. Significantly high or low observed turnover based on comparison with three-bootstrapped test distribution are shown in Tab. 1, 2 and 3.

Turnover can also be regarded as a disruption of equilibrium species diversity caused by phases in which multiple extinctions are followed by appearances of new taxa by waves of immigration or by local evolution. Accordingly, it is interesting to compare the above mentioned results with those obtained from analysing all occurrences at the transition between two successive FUs, based on the number of extinctions of pre-existing taxa and the occurrences of new taxa (bearing in mind the richness of taxa present in both previous as well as successive FUs) (Fig. 5).

The results obtained from the UTI-BU approach indicate that a major turnover pulse took place at the Triversa/Montopoli FU transition. A turnover can be detected at Costa San Giacomo/Olivola FU transition. A weaker turnover is also evident at Farneta/Pirro FU transition where last occurrences prevailed. During the Galerian and the Aurelian MAs real turnover phases cannot be detected. The important middle Galerian faunal renewal is mainly characterised by a high percentage of first occurrences, consequently it may be more representative of a faunal dispersal than an actual turnover pulse. This dispersal is followed by a weak extinction phase at the end of the Galerian MA (Fontana Ranuccio FU), followed by very limited dispersal phases. During the entire Aurelian MA the values of the turnover index progressively decrease and changes in fauna composition are minimal. A minor turnover also characterises the transition from Galerian to Aurelian MAs.

Climate-faunal changes correlation

Similar to results obtained by Foley (1994) and Prado et al. (2001), our analysis reveals that climatic change is not a simple phenomenon, and that different patterns of climatic-faunal evolutionary interactions can be expected depending upon which climatic variables are used. Following Foley (1994), the results of the ETI analysis (diversity and turnover patterns) were correlated with climatic changes represented by isotopic curves. Variables used for this analysis include: number of climatic cycles, maximum δ^{18}O, minimum δ^{18}O, modal temperature, magnitude of climatic variation (maximum temperature - less minimum temperature), and magnitude of climatic change (modal temperature of one period less the modal temperature from the preceding period). The correlation between these variables and both standing richness and the and disappearances rate quotients was explored using the matrix shown in Tab. 4a. The climate of the last 3.5 Ma (it is not available a complete one for 6 Ma) shows a gradual transition between cooler conditions during the Villafranchian to more temperate conditions during the Holocene times. Significant relationships are found between time and maximum δ^{18} O for each period (Tab. 4b). A significant association is also found between maximum δ^{18} O values and climatic variation. Although temperature variables are closely related to each other, the magnitude of change, and the variability in climate and climatic stability are not significantly correlated. In addition, a significant correlation indicates an association between both variables (magnitude of climatic variation and magnitude of climatic change), but does not imply causality. In the same way, it must be noted that a lack of a significant correlation does not necessarily mean that there is no correlation between variables.

The climatic hypothesis predicts that a significant statistical relationship should occur between climatic and faunal events. A number of interesting patterns emerge in this analysis. There is a significant positive correlation between RQf and climatic variation in each interval. Standing richness is also positively correlated with the minimum δ^{18} O values. The positive relationship observed between both variables is statistically significant, $p < 0.05$ and $p < 0.01$, respectively (Tab. 4c).

Discussion

Changes of fauna composition and community structure over time can be inferred by analysis of mammalian richness. Richness and the inter-relationships among rates of origination or immigration and rates of extinction or emigration are dependent upon the relative quality of the sample. Evaluation of the actual diversity at a given interval may be hindered by such problems as gaps or missing time intervals in the fossil record, different taphonomic biases of each mammal group, random factors, or by poor or controversial knowledge about the systematic position of some taxa. Nevertheless, by using more than one methodological approach it is possible to see the following more clearly: 1) faunal variations due to the appearance of new taxa, 2) the ecological vicariance of pre-existing taxa for which there is no substantial change in structure, 3) the appearance of taxa with new adaptive typology and 4) the instances in which there is a significant rate of first occurrences (dispersal) that affect the structure of mammal complexes of Italian peninsula.

In the northwestern Mediterranean area, the high value of first and last occurrences indicates that the faunal renewal from the Miocene to Ruscinian was a marked turnover pulse and not a dispersal event (Azanza et al. 1999, 2000). The lack of quality data for the Ruscinian mammal of Italy enables us to detect only an apparent decrease in richness, which is suggested by the slight predominance of last occurrences. The patterns created by all methodological approaches are very similar. The turnover pulse at Ruscinian-Villafranchian transition is emphasised in Italian faunas by the lack of data for Early Pliocene mammal assemblages compared with the classic European Ruscinian assemblages. However, this phase in Italy can also be regarded as a true turnover because of the disappearance of many Ruscinian taxa typical of humid and dense forest environment and by the appearance of some taxa that inhabit comparatively open environments (Caloi & Palombo 1996; Torre et al. 2001; Palombo in press). The increase in standing richness from Ruscinian to Villafranchian is emphasised in the ETI approach, while in the UTI-cluster approach, where Ruscinian and Triversa FU local faunas are grouped in a single cluster, a slight reduction in richness can be detected.

As pointed out by several authors, an important faunal renewal marks the transition between Triversa FU and Montopoli FU. During this time, the taxa of wooded habitats disappear and the occurrence of new taxa enriches the percentage of species suggestive of open landscapes (e.g., *Mammuthus meridionalis gromovi* and *Equus livenzovensis*). However, the survival of some herbivores in Montopoli FU and of several carnivores in the Triversa FU reduces the differences between these two faunal complexes. The results of our analyses confirm the relevance of this event, which appears to be a turnover phase if we consider the last occurrences at the end of Triversa FU and the first occurrences at the beginning of the following Montopoli FU. Moreover, this event can be regarded as a starting point for new dispersal phases considering that first occurrences dominate during the Montopoli FU and that richness continues to increase during the Middle and Late Pliocene (Fig. 1). The early-middle Villafranchian paleocommunity reorganisation seems to be correlated with the major pulse in the late Neogene glacial trend, which is followed by a further important climatic crisis and concurrent environmental changes at 3.4/3.3 and 2.7/2.6 Ma. The faunal complex of the Triversa FU (early Villafranchian), though renewed with respect to the Ruscinian faunas, maintains a relatively damp forest character, whereas in the Montopoli FU (early middle Villafranchian) there is a substantial reduction of forest taxa and the appearance of several new herbivores and large-sized mammals (Palombo in press and references therein).

The faunal complexes of the Olivola and Tasso FUs show a marked change in mammal associations due to 1) the disappearance of a majority of the Pliocene species, 2) the widespread appearance of new large carnivores and modern dogs, and 3) to the relative abundance of large herbivores inhabiting open environments. Accordingly, the results of UTI and ETI analyses demonstrate a clear increase in diversity around 1.9-1.7 Ma (Fig. 1). The turnover pulse corresponding to the beginning of late Villafranchian MA is consistent with the high value of both the first and last occurrences index as well as of the turnover index. The so-called "wolf-event" (Azzaroli 1993) has to be regarded not only as a dispersal phase but also as a true turnover pulse, related to the climate changes that occur at the end of Pliocene. These climatic changes produce progressive originations (immigration and local speciation) of taxa – both carnivores as well as herbivores (Palombo et al. 2003).

In the LFAs belonging to Farneta, Pirro and Colle Curti FUs (representing a single cluster according to Palombo et al. in press), most of the typically Villafranchian taxa progressively disappear or appear much less frequently, and the fossil record becomes more discontinuous. Species that are identical to or similar to those of the Galerian Middle Pleistocene progressively begin to appear. First occurrences during this time do not equal last occurrences. For example, the imbalance at Farneta FU is due to the higher value of RQl that marks the beginning of a decline in richness.

The diversity of herbivores, mainly ruminants, noticeably decreases. The decline of ruminants seems to be more important at the genus level during the entire late Villafranchian due to the "wolf event" (Torre et al. 2001). Furthermore, several data seem to confirm the transitional character between typical late Villafranchian and typical Galerian mammal assemblages. The faunal renewal that produced typical Italian Middle Pleistocene Galerian faunas is a gradual phenomenon. Thus the "early Galerian" faunas calibrated with the Jaramillo are more closely related to the late Villafranchian fauna (Farneta and Pirro FUs) than they are to typical Galerian assemblages (Palombo et al. 2003).

In the UTI analysis, the important faunal dispersal that takes place at the end of the Pleistocene is highlighted by the highest value of RQf quotient at Slivia FU. This dispersal is yet more evident in the ETI analysis where the RQf progressively increases from 1.0 to about 0.6 Ma. This dispersal phase is followed by a true turnover documented at Isernia FU, in which the most persistent Villafranchian taxa, mainly carnivores, disappear. Diversity is noticeably high, especially among herbivores (Palombo in press).

The renewal of faunas that occur at the end of the early Pleistocene is related to important variations in climatic conditions and to the cyclicity of climatic fluctuations. The renewal, whether due to local evolution of pre-existing taxa or to immigrations from Asia and/or Central Europe, seems to occur in two successive phases. However, this may be overestimated due to the lack of data for "Ponte Galeria" FU. The opportunity to separate the middle Galerian into three different FUs has to be reconsidered (Palombo in press). In any event, the transition from Early to Middle Pleistocene faunas represents a major community reorganization that depicts a significant progressive rejuvenation coincident with the onset of 100 ka climate cyclicity and vegetation changes related to climate worsening.

At the end of Middle Pleistocene and during Upper Pleistocene no important turnover phase can be detected. Nevertheless, there is an increase in richness observed during the late Middle Pleistocene that is consistent with the improvement of climate condition and, possibly with the fragmentation of environments in the Italian peninsula (Palombo & Mussi 2001).

The discussion above has focused on the actual change in climate measured by temperature. Although temperature does add a degree of stability, it may not be the variable. It is possible to hypothesize that regardless of the direction of change, a decrease in climatic stability is likely to have an effect on diversity. In this analysis, climatic stability is measured in terms of 1) the number of major oscillations or cycles per unit of time, 2) the amount of variation in temperature per unit of time (estimated from the difference between maximum and minimum δ^{18} O values), and 3) the magnitude of change (Table 4a, 4b, 4c).

Conclusion

The results obtained by the different methodological approaches (ETI, UTI-BU and UTI-cluster analyses) are basically concordant and show similar trends. In the case of the UTI-cluster approach, diversity among faunal complexes is less evident than in the other methodological approaches, due to the fewer number of intervals analysed. On the other hand, the UTI-BU methodological approach seems to highlight the renewal phases that correspond to the most important faunal reconstructions.

Results of the analyses confirm that the most important faunal renewals take place at: early- middle Villafranchian, middle-late Villafranchian and early-middle Galerian (sensu Gliozzi et al. 1997) transitions. These faunal renewals, due both to originations/immigrations and extinctions + originations/immigrations, can be related to major global climate changes.

Early- middle Villafranchian transition: Pliocene climate worsening corresponds to a turnover phase if we consider the last occurrences at the end of Triversa FU and the first occurrences at the beginning of the following Montopoli FU. Moreover, this event can be considered as a starting point for new dispersal phases given that first occurrences outnumber last occurrences during the Montopoli FU and richness continues to increase during the Middle and Late Pliocene.

Middle-late Villafranchian transition: around 1.9-1.7 Ma (Olivola and Tasso FUs) both a clear increase in diversity and a turnover pulse (high value of both first and last occurrences index as well as of turnover index) can be detected. The so-called "wolf-event" has to be regarded not only as a dispersal phase but also as a true turnover pulse, related to the climate changes occurring at the end of Pliocene

Early-middle Galerian transition: the transition from Early to Middle Pleistocene faunas represents a major community reorganization (dispersal followed by a turnover phase) that shows a significant a progressive rejuvenation coincident with the onset of 100 ka climate cyclicity and vegetation changes related to climate worsening.

We also can observe that the major turnover pulses do not always correspond to high diversity phases. Moreover, a faunal turnover usually marks the beginning of a more or less long period of richness increase, which is followed by period of decreasing richness. Accordingly, it seems that in some cases an environmental change encourages a more efficient exploitation of resources, which gives rise to an increase in mammal diversity and richness.

The results obtained support the argument that climatic changes are a forcing factor in the first appearances (Nf and RQf, including migrations) of mammal taxa.

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Addenda. Subsequent to the submission of the manuscript a revision of the late Middle Pleistocene LFAs from Campagna Romana domonstred that LFAs previously ascribed to Torre in Pietra and Vitinia FUs have to be referred to a single FU (Torre in Pietra FU) (Palombo, Millis & Rosa in press. Remarks on the late Middle Pleistocene biochronology of mammalian faunal complesces of the Campagna Romana - *Geologica Romana*, 37). The new biochronological settings does not substantially affect our results.

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