

LARGE MAMMAL DIVERSITY AND TURNOVER PATTERNS DURING THE PLIO-PLEISTOCENE IN NORTHWESTERN MEDITERRANEAN AREA

B. Azanza^{1,2}, M. T. Alberdi¹ and J. L. Prado³

¹ *Departamento de Paleobiología, Museo Nacional de Ciencias Naturales, CSIC. José Gutiérrez Abascal, 2. 28006-Madrid (Spain). E-mail: malberdi@mncn.csic.es*

² *Departamento de Ciencias de la Tierra, Universidad de Zaragoza, 50009-Zaragoza (Spain). E-mail: azanza@posta.unizar.es*

³ *INCUAPA- Departamento de Arqueología, Universidad Nacional del Centro UNC, Del Valle 5737, 7400-Olavarría (Argentina)*

Abstract: Patterns of large mammal species diversity and turnover in Northwestern Mediterranean area were assessed over the last 6 Ma. Two alternative approaches are considered here based on unequal (biochronological units) and equal time intervals, which were established by multivariate methods using similarity and parsimony respectively. Data quality was estimated in order to evaluate the constraints of the patterns due to a biased, incomplete record in terrestrial deposits. Diversity was standardised by standing richness which calculated species richness at the midpoint of a time interval. Faunal turnover through time was measured as rate quotient normalised for the difference in duration and number of contained taxa among the time intervals. The patterns resulting from both approaches are very similar. The discrepancies between them are higher during the Villafranchian and the Ruscianian, because selected time intervals are very dissimilar and large mammal locality age determinations are scarce. Three biotic events show significant and robust turnover with respect to sampling: the turnover at the Mio-Pliocene transition, the dispersal event at the beginning of the Villafranchian and the turnover around 1.0 Ma. These events are coincident in time with the major pulses of the latest Neogene glacial trend.

Key-words: Diversity, Turnover pulses, Large mammals, latest Miocene, Pliocene, Pleistocene, Northwestern Mediterranean.

Resumen: Se evalúan los modelos de recambio y diversidad faunística en las comunidades de grandes mamíferos del Mediterráneo noroccidental durante los últimos 6 Ma. Dos análisis alternativos se han llevado a cabo, uno con intervalos de tiempo desiguales (unidades biocronológicas) y otro con intervalos iguales, establecidos mediante el uso de métodos multivariantes de similitud y parsimonia respectivamente. Los resultados de ambos análisis muestran mayores discrepancias durante el Villafranchiense y el Rusciniense que durante el Galeriense, debido a una mayor desigualdad entre la duración temporal de los intervalos y a la falta de dataciones en las localidades del Rusciniense. El análisis efectuado con intervalos desiguales indica valores más altos de diversidad desde el Mioceno final al Pleistoceno inferior, aumentando ligeramente en el intervalo 3,5 - 2,0 Ma y disminuyendo posteriormente hasta alcanzar el mínimo al final del Villafranchiense. El análisis efectuado con intervalos iguales indica, a su vez, un ligero incremento de la diversidad al inicio del Rusciniense y otro más pronunciado durante el Villafranchiense inferior y medio. Sin embargo, el descenso de diversidad durante el Villafranchiense superior es menos dramático. Durante el Galeriense ambos análisis señalan que la diversidad aumenta fuertemente y posteriormente decae hasta los niveles actuales. El conjunto de los datos sugiere un débil recambio faunístico al inicio del Rusciniense coincidente con cambios significativos en el medio físico evidenciados durante la transición mio-pliocena (alrededor de 5,4 Ma) e interpretados como un primer pulso de las tendencias glaciares del Neógeno final. El máximo de la diversidad en torno a 3,0 Ma se corresponde con un importante incremento de primeras apariciones. Más que un recambio faunístico, nuestros resultados evidencian la importancia de los eventos de dispersión durante el Villafranchiense inferior en consonancia con la tendencia glacial entre 3,0-2,6 Ma. La caída de diversidad en el Villafranchiense superior es coincidente con una tasa de extinción más alta que la de aparición en el análisis efectuado con intervalos desiguales. En contraste, ambas tasas son similares en los resultados del análisis efectuado con intervalos iguales, lo que parece estar de acuerdo con una pérdida de diversidad menos dramática según este análisis. Desde el inicio del Galeriense, entorno a 1,0 Ma, ambos análisis revelan valores significativamente altos de las primeras apariciones, lo cual es coherente con el aumento pronunciado de la diversidad. Entorno a 1,0 Ma se ha detectado un máximo glacial atribuido al aumento de las capas de hielo del Hemisferio Norte. La coincidencia temporal de estos eventos bióticos con los cambios climáticos globales sugiere una correlación entre ellos.

Palabras-clave: Diversidad, Recambios faunísticos, Grandes mamíferos, Mioceno tardío, Plioceno, Pleistoceno, Mediterráneo noroccidental.

Azanza, B., Alberdi, M. T. and Prado, J. L. (1999): Large mammal diversity and turnover patterns during the Plio-Pleistocene in Northwestern Mediterranean area. *Rev. Soc. Geol. España*, 12(1): 113-122.

Over the past several decades, paleontologists have learned much about origin, causes and patterns of taxonomic diversity, but we do not have enough empirical studies of the biotic history to explain the regulation and maintenance of diversity with respect to time. Four major models have been formulated to explain diversity: (1) "Continuous Diversification" model, (2) "Stationary" model whereby diversity is regulated primarily by density-independent factors of the physical environment, (3) "Red Queen hypothesis" whereby an equilibrium diversity is assumed to be maintained by density-dependent extinction and origination and by coevolution, and (4) "Turnover-pulse hypothesis" whereby climatic change is a driving force in diversity change (MacArthur, 1969; Van Valen, 1973; Rosenzweig, 1975; Levinton, 1979; Stenseth and Maynard Smith, 1985; Vrba, 1985, 1995). All these models and their implied assumptions require testing by use of data from the fossil record at global, continental or regional scales. This record can at least respond if diversity has continued to increase, if little or major climatic change largely control diversity, if coordinated stasis and equilibrium are the rule or the exception, and if density-dependent extinction and origination hold true. In principle, testing can be made both by modelling and by comparative tests.

Available data of Plio-Pleistocene mammal species from the Northwestern Mediterranean area offer opportunities to make a comparative test and to understand the constraining effects of both biotic interaction and abiotic features of the physical environments for mammalian community structure. In the more recent history of the Mediterranean area a number of large scale biotic crises have been proposed as being closely related to major pulses of the Late Cenozoic glacial trend (Aguirre *et al.*, 1976; Aguirre and Morales, 1990; Azzaroli, 1983; Azzaroli *et al.*, 1988; Steininger *et al.*, 1985; Sala *et al.*, 1992; Torre *et al.*, 1992). The aforementioned studies referred to this time interval focused on biochronology and biogeographical patterns: the aim of this paper is to discuss the patterns of faunal turnover and changes in species diversity that happened at the interval following the Messinian crisis, but we are not concerned here with its effect on community ecology.

Two alternative approaches are considered based on unequal (biochronological units) and equal time intervals in order to analyse diversity and turnover through time. One of the purposes of this paper is to evaluate the relative importance of the faunal restructurations possibly associated with major changes in environmental conditions, which are

assumed to occur at the boundaries between biochronological units (Alberdi *et al.*, 1997).

Biochronological framework

A major problem in the design of a comparative test is how to control the variation in diversity and turnover through time. The traditional diversity study employs generally recognised biochronological units. Different methodological approaches used to establish a biochronological scale have been proposed for the Plio-Pleistocene formations of the Northwestern Mediterranean area (Ambrosetti *et al.*, 1972; Mein, 1975, 1990; Azzaroli 1977, 1982, 1983; Guérin, 1982; Aguilar and Michaux, 1987; Agustí *et al.*, 1987; De Bruijn *et al.*, 1992). However, none of them extends through the complete interval of time analysed here and there are discrepancies among them making it difficult to establish a consensus. In addition, the boundaries among them are not defined with regard to faunal turnover. Thus, the use of previous biochronological scales represented a problem because of the possibility of creating fictitious events at these boundaries. The use of equal intervals could be an alternative approach, but this requires precise ordering of first and last appearance events of taxa, and a good calibration of the event sequence with respect to time.

Unequal time interval (UTI) approach

Biochronological units (BUs) are assumed to represent "lapses of time during which faunas have certain taxonomic homogeneity, the discontinuity between them corresponding to faunal restructurations associated with major changes in environmental conditions" (Alberdi *et al.*, 1997), converging with d'Orbigny's concept of *Étage* and *Subétage* (equivalent to the concept of Ecological Evolutionary Unit and Subunit of Boucot, 1990).

Alberdi *et al.* (1997) proposed an integrated multivariate approach combining cluster analysis and non-linear ordinations that allows for the recognition of a succession of faunal complexes having certain taxonomic homogeneity (i.e. BUs). Nine biochronological units (A to I) are recognised during the last six million years (Fig. 1). The duration of these BUs was estimated from the available datings of localities and varies between 2.5 to 0.2 Ma.

There is little correspondence between BUs and previous biochronological scales (MN "zones", Mammal Units, biozones). Unit A may be more or less equivalent to MN13 though its lower boundary is not explored. Unit B includes all the Ruscian faunas

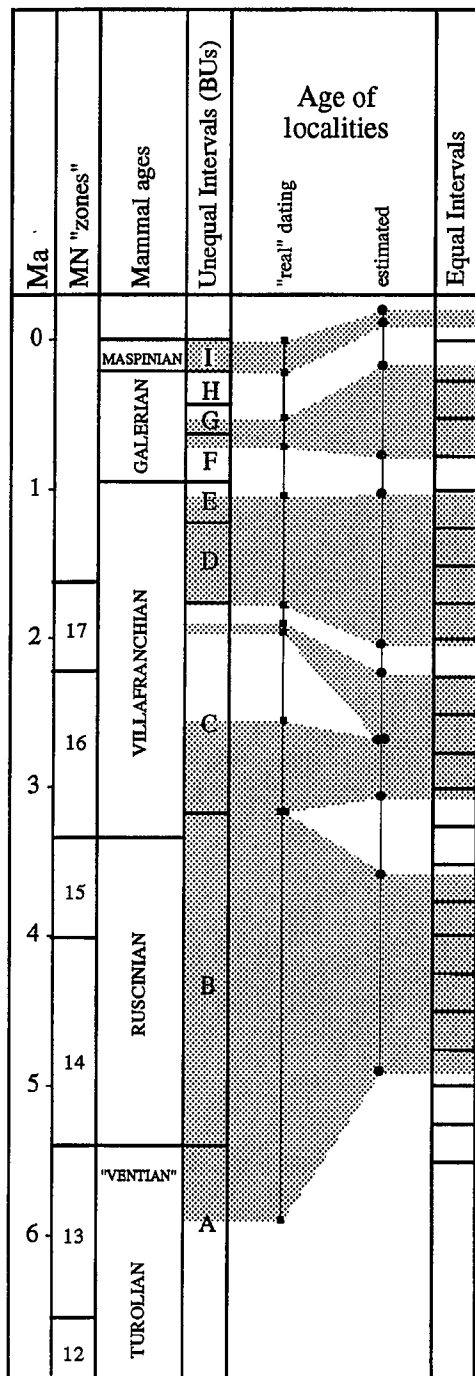


Figure 1.- Biochronological framework. Two alternative approaches are considered based on unequal (biochronological units, Alberdi *et al.*, 1997) and equal time intervals. Calibration of the first and last appearance event sequence is made from radioisotopic and paleomagnetic ages estimated for localities (following Alroy, 1992). Nevertheless, this calibration introduces a temporal distortion that increases as dates become fewer. The distortion between "real" and "estimated" age of localities is expressed graphically.

unit (Azzaroli, 1983). This BU also includes the Tasso faunal unit, thereby not supporting the dispersal event that characterised the beginning of this Italian unit, thus being in agreement with Agustí *et al.* (1987). The subsequent BUs (units E to I) show major correspondence with previous biochronological frameworks (Agustí *et al.*, 1987; Sala *et al.*, 1992).

Equal time interval (ETI) approach

A precise ordering of first and last appearance events of taxa is not achievable directly from the Plio-Pleistocene continental record of the Northwestern Mediterranean area, because most data come from isolated localities and age calibrations are scarce. The parsimony-based method of "Disjunct Distribution Ordination" developed by Alroy (1992) are used to solve these problems (Azanza *et al.*, 1997). The chronological relationship can be demonstrated without the use of stratigraphic data simply by detecting which taxa have overlapping (conjunct) or non-overlapping (disjunct) distributions across sets of taxonomic lists (Alroy, 1992, 1994). The succession of local faunal assemblages is greatly coincident with the previous results. Two major discrepancies are worth mentioning: Venta Micena should be moved from unit D to unit E, or even to unit F, and both Isernia and L'Aragó from unit H to unit G. Calibration of the appearance event sequence is possible from radioisotopic and paleomagnetic ages estimated for localities. Nevertheless, this calibration introduces a temporal distortion that has been expressed graphically in figure 1. It is a problem to define an optimal interval length. The order of magnitude corresponding to the shortest length of the biochronological units (0.25 Ma.) was selected in order not to hide evolutionary events.

Methodology applied to the analysis of faunal change

Faunal changes in Plio-Pleistocene mammal communities from the Northwestern Mediterranean area occurs as diversity changes and turnovers. The analyses were performed using the compilation formed recently by Alberdi *et al.* (1997, table 2). An estimation of the quality of the data is needed however in order to evaluate the constraints of these patterns due to a biased, incomplete record in terrestrial deposits.

Data quality

The number of coexisting species show important fluctuations among the time intervals. The differences could reflect true richness changes or be due to incomplete sampling. An usual method for a partial correction of the underestimation of richness in a particular interval, is to infer the occurrence of the taxa known from preceding and succeeding intervals or *range-through* taxa. This method, known as the minimum census technique (Rosenzweig and Taylor,

(MN14 + MN15) and that of Triversa (MN16). The MN16 zone does not appear clearly. The great intercontinental faunal dispersal event between Ruscinian and Villafranchian faunas is marking by the arrival into Eurasia of African elephants and North American *Equus* (intra MN16). The rise of unit D is coincident with the so called "Wolf" event at the beginning of the Olivola faunal

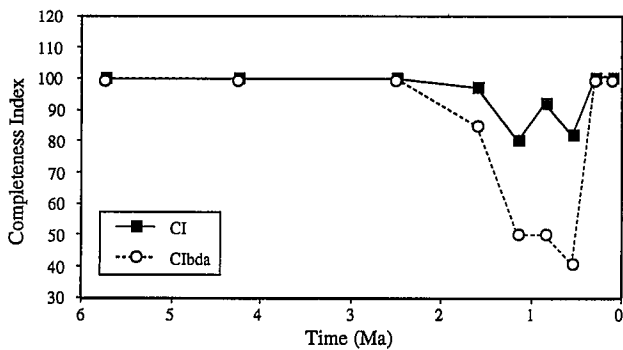


Figure 2.- Mammalian species completeness indices per interval plotted against time interval, using the UTI approach.

1980), is commonly applied in analyses of mammalian richness (Stucky, 1990). The relative sampling quality can be estimated by the proportion of range-through taxa in an interval. Two completeness indices have been proposed (Krause and Maas, 1990; Maas and Krause, 1994; Maas *et al.*, 1995):

$$CI = [N_i / (N_i + N_{rt})] \times 100$$

$$CI_{bda} = [N_{bda} / (N_{bda} + N_{rt})] \times 100$$

where N_i is the total number of species actually found in the interval, N_{rt} is the number of range-through species, and N_{bda} is the number of species that are known before, during, and after the interval. Low index values (< 70 , Maas *et al.*, 1995) are likely to underestimate appearances, disappearances and taxonomic richness of intervals. These indices have not been calculated in the equal time approach.

Diversity

Diversity is used as a general term that refers to the number of taxa in a clade or fauna in a given area during a specific interval of time. Diversity is used here as the concept of richness. Numerous measures of species richness have been proposed, all based ultimately on the number and relative importance of species. None of these methods is without its limitations.

The *species richness* is widely measured from the total number of taxa that actually or potentially occur in each interval. However, this method assumes that all first appearances occur at the beginning of the interval and the last appearances at the end. Thus, the richness in a single time interval could be overestimated by counting taxa as coexisting when actually they did not overlap in time. One of the most common methods for standardisation is to calculate species richness at the midpoint of a time interval. This method, called *standing richness* (Harper, 1975), is a concept similar to the running mean (Webb, 1969). Following Maas *et al.* (1995) we calculated standing richness (N_{sr}) as:

$$N_{sr} = N_{bda} + N_{rt} + 1/2 (N_f + N_l - N_o)$$

where N_f is the number of first occurrences in the time interval, N_l is the number of last occurrences in the time

interval, and N_o is the number of species known only for that time interval.

Turnover

Change in diversity does not necessarily imply restructuring of the mammal communities. According to the equilibrium theory (MacArthur and Wilson, 1967), extinction and origination (immigration and speciation) could occur independently of each other yet yield an equilibrium species diversity. Disruptions of equilibrium could be caused by rapid turnover in which multiple extinctions are followed by a wave of originations. Because *in situ* speciation and immigration may not be distinguishable we treat both as "first occurrences". In like manner, local extinctions are treated as "last occurrences".

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* is a method that attempts to normalise for these biases. The first appearance and last appearance rate quotients (*RQ*) were calculated as the ratio:

$$RQ = R_o / R_e$$

where R_o is the observed number of first or last occurrences and R_e is expected number of first or last appearances. Expected rate is calculated using multiple regression of natural logarithm of observed number of first or last occurrences on the natural logarithm of the duration of the interval (Gingerich, 1987). In the case of the ETI approach, it is not necessary to normalise for interval duration and expected rate is calculated using least-squared regression of natural logarithm of 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 chi-square 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 hypotheses is that first or last occurrences are considered to be equally likely in all intervals and therefore should be distributed evenly among the intervals.

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 or last occurrences are randomly distributed among faunal intervals. The test distribution of each interval consists of expected numbers of first or 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 first occurrence datum and one last occurrence datum, and ranges are not allowed to be truncated.

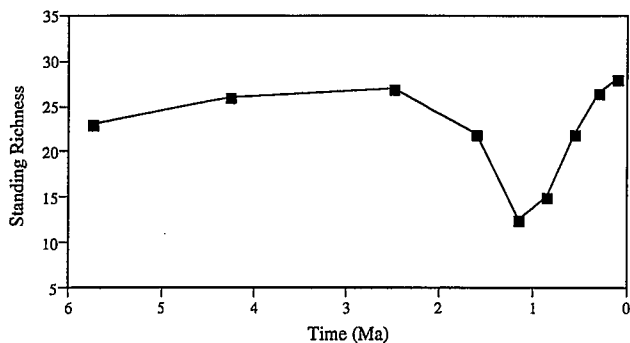


Figure 3.- Standing species richness per interval plotted against time interval, using the UTI approach.

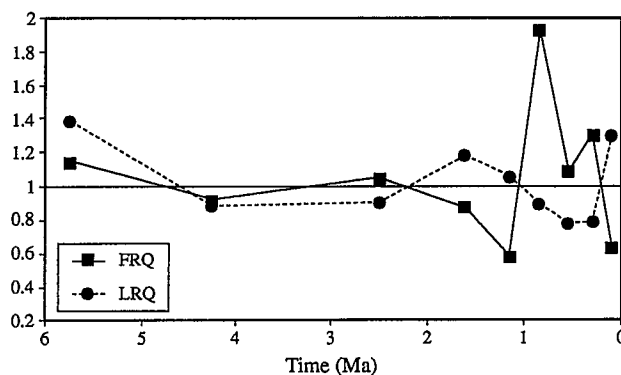


Figure 5.- First (FRQ) and last (LRQ) appearance rate quotients per interval plotted against time interval, using the UTI approach.

Results of the UTI approach

Only the more conservative *Cibda* index shows significant low values with respect to the interval E, F and G (Fig. 2). The low value of interval F was expected because it is between two intervals with a high number of range-through species and in our record there is a low proportion of species present in more than two intervals, and consequently the richness of the intervals E and G could be underestimated. However, during the Quaternary, short-term range fluctuations can be recognized which are closely related to climate oscillations. Thus, the presence or absence of a species may be due merely to shifts in its distribution in and out of the study area. In this situation, the range-through taxa does not always indicate a poor record quality.

The standing richness (Fig. 3 and Table I), is high from the latest Miocene to Early Pliocene increasing slightly in the 3.5 - 2.0 Ma interval (interval C), although the maximum number of species was reached during the Ruscinian (interval B) (Fig. 4). After 2.0 Ma the standing richness begins to decline reaching its minimum at the end of the Villafranchian (interval E), despite most of the families being recorded. During the Late Pleistocene it increases strongly (intervals F to I), later falling to the present diversity.

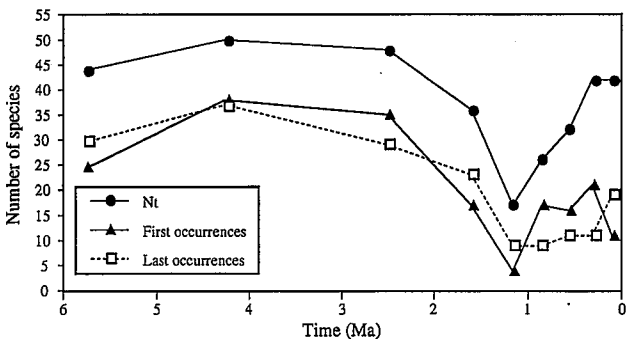


Figure 4.- Maximum number of species (Nt) and the first- and last occurrences per interval plotted against time interval, using the UTI approach.

Although the first- and last-appearance rate quotients (FRQ and LRQ respectively) track one another closely during the latest Miocene to Early Pliocene (Fig. 5), during the latest Turolian (interval A) the last occurrences surpass the first occurrences, both in total number (Fig. 4) and in RQ. This situation is compensated during the Ruscinian (unit B) by a higher increase of first than last occurrences, the FRQ and LRQ being similar. This tendency is maintained during the Villafranchian where first occurrences clearly surpass last occurrences. This situation is coincident with a slight increase in standing richness. At the end of the Villafranchian (units D and E) this tendency is disrupted. The Late Villafranchian drop in richness is coincident in the UTI approach with higher values of LRQ than of FRQ. From the beginning of the Galerian, around 1 Ma, there are significantly high values of FRQ, which is coherent with the increase in standing richness at this time.

Tests for first occurrences yielded significant values at only $p < 0.09$ while for last occurrences yielded at $p < 0.5$ ($\chi^2 = 13.86$ for first occurrences, and $\chi^2 = 7.42$ for last occurrences, d.f.=8) This does not lead us to reject the null hypothesis that last or first occurrences are distributed evenly among the intervals. Nevertheless, the Galerian turnover contributed the most to the first occurrences chi-square value, whereas the latest Miocene and Maspinian provided the greatest part of the last occurrences chi-square value.

In contrast, the bootstrapping tests (Table I) showed a significantly high number of first occurrences in intervals C ($p < 0.05$) and F ($p < 0.01$), a very significant low number of first occurrences in the intervals E ($p < 0.001$) and I ($p < 0.01$), a significant high number of last occurrences in intervals A ($p < 0.05$) and B ($p < 0.01$), and a significant low number of last occurrences in G ($p < 0.01$), H ($p < 0.001$) and I ($p < 0.05$).

Results of the ETI approach

In addition to the Galerian peak, the ETI approach has revealed another pronounced increase in standing

Zone	Duration (Ma)	Nt	Nrt	No	Nbda	CI	CIbda	Nsr	First occurrences				Last occurrences					
									Obs.	Exp.	χ^2	RQ	Obs.	Exp.	χ^2	RQ		
A	0.7	44	0	13	2	100	100	23	25	21.81	0.47	1.15		30	21.70	3.18	1.38	(+)
B	2.3	50	0	25	1	100	100	26	38	41.19	0.25	0.92		37	41.71	0.53	0.89	(++)
C	1.2	48	0	20	5	100	100	27	35	33.46	0.07	1.05	(+)	29	32.08	0.30	0.90	
D	0.6	36	1	10	6	97	86	22	17	19.33	0.28	0.88		23	19.42	0.66	1.18	
E	0.3	17	4	4	4	81	50	12,5	4	6.90	1.22	0.58	(--)	9	8.48	0.03	1.06	
F	0.3	26	2	4	2	93	50	15	17	8.80	7.63	1.93	(++)	9	10.01	0.10	0.90	
G	0.3	32	7	7	5	82	42	22	16	14.68	0.12	1.09		11	14.16	0.71	0.78	(--)
H	0.2	42	0	3	12	100	100	26,5	21	16.02	1.55	1.31		11	13.93	0.62	0.79	(--)
I	0.2	42	0	4	15	100	100	28	11	17.25	2.26	0.64	(--)	19	14.64	1.30	1.30	(-)
										Chi-square		13.86		Chi-square		7.41		
										Sig. level		0.0856		Sig. level		0.4925		

Table I. Mammalian specific turnover and richness for the 9 unequal time intervals (biochronological units) recognized from the latest Miocene to Recent in the Northwestern Mediterranean area (Alberdi *et al.* 1997). N_t: number total of species, N_{rt}: number of species range through time; N_o: number of species known only; N_{bda}: number of species recorded before, during, and after an interval; CI, CI_{bda}: completeness indices; and N_{sr}: standing richness. Obs.: observed, Exp.: expected. Expected first appearances were calculated as: $Re = \exp [0.397 \ln(\text{duration}) + 1.335 \ln(\text{Nsr}) - 0.962]$ and expected last appearances were calculated as: $Re = \exp [0.456 \ln(\text{duration}) + 0.906 \ln(\text{Nsr}) + 0.399]$. 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 $p < 0.05$.

richness during the Early and Middle Villafranchian while the Late Villafranchian drop is less dramatic (Fig. 6). Whilst the total number of species is also high during the latest Miocene (Fig. 7), in the standing richness this does not appear clearly.

As in the UTI approach, FRQ and LRQ track one another closely during the latest Miocene to Early Pliocene suggesting that a broad range of rates are possible within the equilibrium. Nevertheless, a weak turnover pulse at the beginning of the Ruscinian, could be indicated by the high values of both FRQ and LRQ (Fig. 8). During the Early Villafranchian the equilibrium is disrupted, with the FRQ higher in accordance with the acme of standing richness near 3.0 Ma. In contrast to the UTI approach, FRQ and LRQ track one another closely during the Late Villafranchian. This seems to be in agreement with a less dramatic drop in standing richness (Fig. 6). As before, the ETI approach also reveals significantly high values of FRQ around 1 Ma, in coincidence with the pronounced increase in standing richness.

First and last appearances were significantly heterogeneous among intervals ($\chi^2 = 45.15$ for first appearances and $\chi^2 = 63.34$ for last appearances; $p < 0.01$ and d.f. = 21), leading us to reject the null hypothesis. The results in the bootstrapping analysis are given in Table II, only the intervals corresponding to the Ruscinian transition show very significant high number of last appearances.

Discussion

Analysis of turnover and richness patterns provides an important tool in formulating hypotheses of community evolution. The analysis of turnover patterns in this paper takes into account whether turnover

represents replacement by ecological vicariants or introduction of new adaptive types (Maas *et al.*, 1995). These analyses can potentially provide information first for determining the saturation level and number of empty niches within a community (Walker and Valentine, 1984), and second for understanding the constraining effects of both biotic interaction and abiotic features of the physical environment for different habitats (Stucky, 1990). There are several problems affecting turnover patterns related to the poorly known systematic positioning of many species, gaps or missing time intervals in the fossil record (Flessa and Jablonski, 1983) and also the apparent absences or "Lazarus effect" (Jablonski, 1986). Because different groups of mammals have different taphonomic biases and may vary in abundance between stratigraphic horizons, the change in diversity among intervals are sensitive to the quality of the data. With these limitations in mind, we focus on the biotic events from the latest Miocene to the Holocene in the Western Mediterranean area, where turnover was both significant and robust with respect to sampling. These episodes of faunal changes correspond in time with significant changes in the physical environment as several lines of evidence indicated.

The latest Miocene (unit A, 6.1 - 5.4 Ma) corresponds to the Messinian salinity crisis (Aguirre *et al.*, 1976; Cita *et al.*, 1995). It has been postulated that this desiccation phase in the Mediterranean Sea provided a number of migration possibilities for land mammals between Africa and Eurasia. African species appear to have migrated across the Iberian Peninsula to Eurasia. This was reflected in the faunal composition by an unusual record of camels and hippopotamus (Pickford *et al.*, 1995). Nevertheless, some immigrations may have taken place before the Messinian crisis (Pickford *et al.*, 1995; Agustí and Lle-

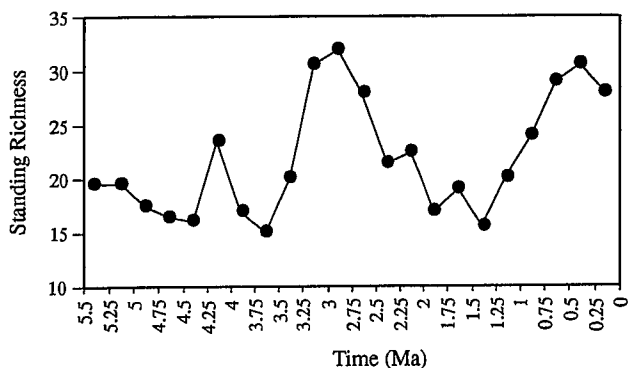


Figure 6.- Standing species richness per interval plotted against time interval, using the ETI approach.

nas, 1996). The latter mentioned authors rule out the possibility of interchange with Africa, given that these taxa could have come across from Eurasia. Alternative interpretations have been put forward for the Messinian evaporites that may not imply desiccation of the deep Mediterranean (Martínez del Olmo, 1996; Michalzik, 1997). In turn, the pattern of turnover shows high values of first and last appearances that may indicate more a turnover pulse than a dispersal event at the Mio-Pliocene transition. During the early Pliocene the total number of species reached a maximum. Some families (Orycteropodidae, Giraffidae, Viverridae, Tapiridae, Cercopithecidae) appeared in this interval, of which Tapiridae is also present during unit C and Cercopithecidae in all of the following intervals. Despite the high diversity, Camelidae and Hippopotamidae, that were present before, are absent in the Ruscinian. In contrast, the values of standing

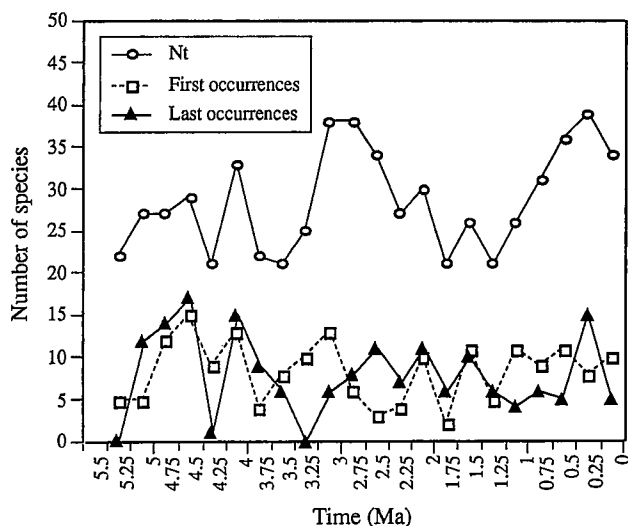


Figure 7.- Maximum number of species (Nt) and the first- and last appearances per interval approach plotted against time interval, using the ETI approach.

richness indicate a trend towards increasing diversity which peaks in the Villafranchian (unit C, 3.1 - 1.9 Ma). The increase of standing richness is emphasised by the ETI approach where, near 3.0 Ma, the first of the two maximum peaks was reached, recorded for the total time analysed in spite of a loss of family diversity. Despite the acme in diversity, first and last occurrences do not differ significantly from the expected values and similar results are obtained in the bootstrapping analysis. This major biotic event corresponds to the so-called *Equus*-elephant event during the lower Villafranchian (Steininger *et al.* 1985; Azzaroli *et al.*, 1988). The results obtained confirm the relevance of this dispersal event.

After 1.9 Ma there is a clear decrease in the diversity (units D and E). The beginning of unit D corresponds to the faunal transition, the so-called "Wolf" event (Azzaroli, 1983). There is no strong evidence of this dispersal event. First occurrences in unit E are significantly low according to bootstrapping analysis. This result should be expected because of the low completeness index. Nevertheless, some qualifications must be made. During the Quaternary, the absence of taxa could be due to short-term range fluctuations which tracked climatic oscillations. This could be the case of this unit, where the true absence of some lineages has been verified, such as the family Suidae in Europe (Made, 1989-90).

The beginning of unit F (around 1 Ma) corresponds to the main disruption observed among the faunal assemblages analysed here. The rate quotient and bootstrap analysis indicates significant turnover at the beginning of the Galerian due to the high number of first occurrences. At this moment, a great part of the lineages that comprise modern mammal communities appear, humans included. This turnover represented a major community reorganization that showed a total rejuvenation of the fauna and is coincident with cooler and drier conditions, the so-called "Glacial Pleistocene" (Shackleton, 1984; Shackleton and Hall, 1984). Despite the richness, it could nevertheless be underestimated since unit G has a low completeness index, with the tendency to increase diversity being maintained through the Late Pleistocene, accomplished by significant low numbers of last occurrences in units G and H (0.7 - 0.2 Ma). During unit I the second of the two maximum peaks was reached.

At the end of the Pleistocene the ETI approach revealed a clear trend of decreasing diversity which has accelerated up to present time. This trend is coincident with a highly significant low number of first occurrences in the UTI approach. In contrast, last occurrences were higher than expected in the ETI approach. The last event corresponds to the Late Pleistocene extinction, due to both hunting by prehistoric humans or climatic changes (Martin and Klein, 1984; Barnosky, 1986), but the intensity seem not to be as marked in the Northwestern Mediterranean area as it is in other regions of the world.

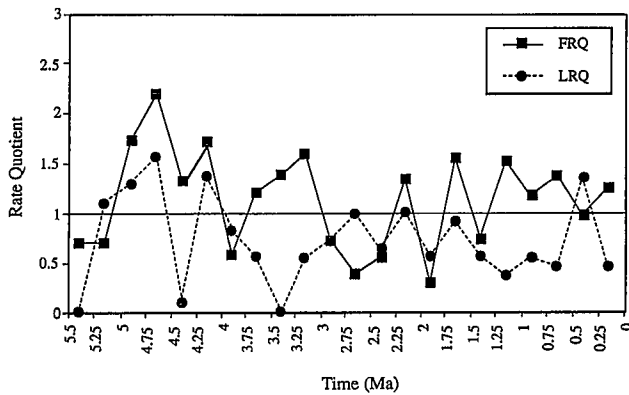


Figure 8.- First (FRQ) and last (LRQ) appearance rate quotients per interval plotted against time interval, using the ETI approach.

Conclusion

Patterns of large mammal species turnover and richness were assessed from the latest Miocene to Holocene in the Western Mediterranean area. Two alternative approaches are considered here based on unequal (biochronological units) and equal time intervals (UTI and ETI respectively), which were established by multivariate methods using similarity and parsimony respectively. The discrepancies between the two approaches are higher during the Villafranchian and the Ruscian than during the Galerian, because selected time intervals are very dissimilar and no age determinations of large mammal localities are available during the Ruscian. In both the UTI and ETI approaches, only three biotic events show significant and robust turnover with respect to sampling.

The first event has classically been interpreted as a dispersal event between Eurasia and Africa, favoured by the desiccation of the Mediterranean Sea. The pattern of turnover shows high values of first and last occurrences that may indicate rather a turnover pulse than a dispersal event.

The second major biotic event resulting from our analyses corresponds to the so-called *Equus*-elephant event during the lower Villafranchian. The results obtained confirm the relevance of this dispersal event that signified a marked increase in diversity due to the high number of first occurrences.

The turnover pulse at around 1 Ma represents the last major biotic event in Europe. This turnover represented a major community reorganization that showed a total rejuvenation of the fauna.

These biotic events correlate clearly with climatic changes. Several lines of evidence indicate that 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 glaciation trends. Between 3.0-2.6 Ma the onset of bipolar glaciation occurred followed by glacial-interglacial cycles of moderate amplitude sustained at the orbital periodicity of 41 ka (Williams *et al.*, 1988). After 0.9 Ma glacial maxima

became more extreme and the dominant periodicity of variation shifted to 100 ka attributed to massive Northern Hemisphere ice sheets (Suc *et al.* 1995; Shackleton 1995).

The authors wish to express their thanks to Drs. M. Maas and J. Alroy for valuable suggestions about their analytical programs, and to Dr. C. Howell and E. Cerdeño for their critical revision of the manuscript and critical discussions. Dr. M. Pickford corrected the English. The present work was made possible by the following research grants: PB91-0082 and PB94-0071 of DGICYT, and the IberoAmerican Cooperation Program, MEC, Spain, and UNC-grant to JLP, Argentina.

References

- Aguilar, J.-P. and Michaux, J. (1987): Essai d'estimation du pouvoir séparateur de la méthode biostratigraphique des lignées évolutives chez les Rongeurs néogènes. *Bull. Soc. Géol. France*, (8), 3 (6): 1113-1124.
- Aguirre, E., López, N. and Morales, J. (1976): Continental faunas in Southeast Spain related to the Messinian. *Il significato Geodinamico della crisi di Salinità del Miocene terminale nel Mediterraneo*, Messinian Seminar, 2, Gargano, September 5-12, 1976: 62-63.
- Aguirre, E. and Morales, J. (1990): Villafranchian Faunal Record of Spain. *Quartärpaläontologie*, 8: 7-11.
- Agustí, J. and Llenas, M. (1996): The late Turolian murid rodent succession in eastern Spain. *Acta zool. cracov.*, 39: 47-56.
- Agustí, J., Moyà-Solà, S. and Pons, J. (1987): La sucesión de mamíferos en el Pleistoceno inferior de Europa: proposición de una nueva escala bioestratigráfica. *Paleont. i Evol.*, 1: 287-295.
- Alberdi, M.T., Azanza, B., Cerdeño, E. and Prado, J.L. (1997): Similarity relationship between Mammal faunas and biochronology from latest Miocene to Pleistocene in Western Mediterranean area. *Eclog. Geol. Helvet.*, 90: 115-132.
- Alroy, J. (1992): Conjunction among taxonomic distributions and the Miocene mammalian biochronology of the Great Plains. *Paleobiology*, 18(3): 326-343.
- Alroy, J. (1994): Appearance event ordination: a new biochronologic method. *Paleobiology*, 20(2): 191-207.
- Ambrosetti, P., Azzaroli, A., Bonadonna, F.P. and Follieri, M. (1972): A scheme of Pleistocene chronology for the Tyrrhenian side of Central Italy. *Boll. Soc. Geol. Italia*, 91: 169-184.
- Azanza, B., Alberdi, M.T., Cerdeño, E. and Prado, J.L. (1997): Biochronology from Latest Miocene to Middle Pleistocene in the Western Mediterranean Area. A Multivariate Approach. In: *Actes du Congrès Biochron'97*. (J.L. Aguilar, S. Legendre and J. Michaux, Eds.), *Mém. Trav. E.P.H.E., Inst. Montpellier*, 21: 567-574.
- Azzaroli, A. (1977): The Villafranchian Stage in Italy and the Plio-Pleistocene Boundary. *Giorn. Geol.*, 41: 61-79.
- Azzaroli, A. (1982): Remarques sur les subdivisions chronologiques du Villafranchien. *Actes Coll. "Le Villafranchien Méditerranéen"*, Lille 9-10 décembre 1982, 1: 7-14.
- Azzaroli, A. (1983): Quaternary mammals and the "End-Villafranchian" dispersal event - A turning point in the history of Eurasia. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 44: 117-139.

Interval	N _i	N _o	N _{bd}	N _{sr}	First appearances				Last appearances					
					Obs.	Exp.	χ^2	first RQ	Obs.	Exp.	χ^2	last RQ		
5.5 - 5.25	22	0	17	19.5	5	7.22	0.68	0.69		0	10.98	10.98	0.00	(-)
5.25 - 5	27	2	12	19.5	5	7.22	0.68	0.69	(---)	12	10.98	0.10	1.09	(+)
5 - 4.75	27	7	8	17.5	12	7.00	3.57	1.71		14	10.93	0.86	1.28	(++)
4.75 - 4.5	29	9	5	16.5	15	6.88	9.58	2.18	(+)	17	10.91	3.40	1.56	(+++)
4.5 - 4.25	21	0	11	16	9	6.82	0.70	1.32		1	10.89	8.90	0.09	(---)
4.25 - 4	33	9	14	23.5	13	7.63	3.79	1.70		15	11.06	1.41	1.36	(+)
4 - 3.75	22	1	11	17	4	6.94	1.25	0.58		9	10.92	0.34	0.82	(+)
3.75 - 3.5	21	2	9	15	8	6.69	0.26	1.20		6	10.87	2.18	0.55	
3.5 - 3.25	25	0	15	20	10	7.28	1.02	1.37		0	10.99	10.99	0.00	(---)
3.25 - 3	38	4	23	30.5	13	8.23	2.77	1.58		6	11.17	2.39	0.54	(-)
3 - 2.75	38	2	26	32	6	8.34	0.66	0.72	(-)	8	11.19	0.91	0.71	
2.75 - 2.5	34	2	22	28	3	8.03	3.15	0.37	(--)	11	11.13	0.00	0.99	
2.5 - 2.25	27	0	16	21.5	4	7.43	1.58	0.54	(-)	7	11.02	1.47	0.64	
2.25 - 2	30	6	15	22.5	10	7.53	0.81	1.33		11	11.04	0.00	1.00	
2 - 1.75	21	0	13	17	2	6.94	3.52	0.29	(--)	6	10.92	2.22	0.55	
1.75 - 1.5	26	7	12	19	11	7.17	2.05	1.53	(+)	10	10.97	0.09	0.91	
1.5 - 1.25	21	0	10	15.5	5	6.76	0.46	0.74		6	10.88	2.19	0.55	
1.25 - 1	26	3	14	20	11	7.28	1.90	1.51	(+)	4	10.99	4.44	0.36	(-)
1 - 0.75	31	1	17	24	9	7.67	0.23	1.17		6	11.07	2.32	0.54	(-)
0.75 - 0.5	36	2	22	29	11	8.11	1.03	1.36		5	11.15	3.39	0.45	(--)
0.5 - 0.25	39	6	22	30.5	8	8.23	0.01	0.97		15	11.17	1.31	1.34	
0.25 - 0	34	3	22	28	10	8.03	0.49	1.25		5	11.13	3.38	0.45	(---)
						Chi-square	40.17				Chi-square	63.36		
						Sig. level	0.0071				Sig. level	0.0001		

Table II. Mammalian specific turnover and richness for the 22 equal time intervals recognized for the last 5.5 Ma. N_i: number of species; N_o: number of species known only; N_{bd}: number of species recorded before, during, and after an interval; N_{sr}: standing richness. Obs.: observed, Exp.: expected. Expected first appearances were calculated as: $Re = \exp [0.291 \ln(N_{sr}) + 1.113]$ and expected last appearances were calculated as: $Re = \exp [0.039 \ln(N_{sr}) + 2.28]$. 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 $p < 0.05$.

- Azzaroli, A., De Giuli, C., Ficarelli, G. and Torre, D. (1988): Late Pliocene to Early Mid-Pleistocene mammals in Eurasia: Faunal succession and dispersal events. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 66: 77-100.
- Barnosky, A.D. (1986): "Big Game" Extinction Caused by Late Pleistocene Climatic Change: Irish Elk (*Megaloceros giganteus*) in Ireland. *Quater. reseach.*, 25: 128-135.
- Barry, J.C., Morgan, M.E., Flynn, L.J., Pilbeam, D., Jacobs, L.L., Lindsay, E.H., Raza, S.M. and Solounias, N. (1995): Patterns of faunal turnover and diversity in the Neogene Siwaliks of Northern Pakistan. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 115: 209-226.
- Boucot, A.J. (1990): Community Evolution: Its Evolutionary and Biostratigraphic Significance. *Paleontol. Soc., Sp. Public.*, 5: 48-70.
- Brujn, H. de, Daams, R., Daxner-Höck, G., Fahlbusch, V., Ginsburg, L., Mein, P. and Morales, J. (1992): Report of the RCMNS working group on fossil mammals, Reisenburg 1990. *Newslett. Strat.*, 26: 65-118.
- Cita, M.B., Rio, D. and Sprovieri, R. (1995): The Pliocene Series: Chronology of the type Mediterranean Record and Standard Chronostratigraphy. In: *Paleoecology, Climate and Sequence Stratigraphy of the Pliocene* (J.H. Wrenn and J.P. Suc, Eds.), *American Association of Stratigraphy and Palynology*, Special Volume.
- Flessa, K.W. and Jablonski, D. (1983). Extinction is here to stay. *Paleobiology*, 9: 315-321.
- Gilinsky, N.L. (1991): Bootstrapping and the fossil record. In: *Analysis Paleobiology* (N.L. Gilinsky and P.W. Signor, Eds.), *Paleontol. Soc. Univ. Tennessee, Knoxville*, 185-206.
- Gingerich, P.D. (1987): Extinction of Phanerozoic marine families. *Geol. Soc. Amer., Abstracts with Programs*, 19: 677.
- Guérin, C. (1982): Première biozonation du Pléistocène européen: principal résultat biostratigraphique de l'étude des Rhinocerotidae (Mammalia, Perissodactyla) du Miocène terminal au Pléistocène supérieur d'Europe occidentale. *Geobios*, 15: 593-598.
- Harper, C.W. Jr. (1975): Standing diversity of fossil groups in successive intervals of geologic time: A new measure. *Jour. Paleobiol.*, 49: 752-757.
- Jablonski, D. (1986): Background and Mass Extinctions: The Alternation of Macroevolutionary Regimes. *Science*, 231: 129-133.
- Krause, D.W. and Maas, M.C. (1990): The biogeographic origins of late Paleocene-early Eocene mammalian immigrants to the Western Interior of North America. In: *Dawn of the Age of Mammals in the Northern Part of the*

- Rocky Mountain Interior, North America* (T.M. Bown and K.D. Rose, Eds.), *Geol. Soc. Amer., Spec. Pap.*, 243: 71-105.
- Levinton, J.S. (1979): A theory of diversity equilibrium and morphological evolution. *Science*, 204: 335-336.
- Maas, M.C. and Krause, D.W. (1994): Mammalian turnover and community structure in the Paleocene of North America. *Hist. Biol.*, 8: 91-128.
- Maas, M.C., Anthony, M.R.L., Gingerich, P.D., Gunnell, G.F. and Krause, D.W. (1995): Mammalian generic diversity and turnover in the Late Paleocene and Early Eocene of the Bighorn and Crazy Mountains Basins, Wyoming and Montana (USA). *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 115: 181-207.
- MacArthur, R.H. (1969): Patterns of communities in the tropics. *Biol. J. Linn. Soc.*, 1: 19-30.
- MacArthur, R.H. and Wilson, E.O. (1967): *The Theory of Island Biogeography*. Princeton University Press, Princeton.
- Made, V. der, J. (1989-90): A range-chart for European Suidae and Tayassuidae. *Paleontol. i Evol.*, 23: 99-104.
- Martin, P.S. and Klein, R.G. (1984): *Quaternary Extinctions, a Prehistoric Revolution*. Tucson, Arizona: University of Arizona Press, 892 pp.
- Martínez del Olmo, W. (1996): Yesos de margen y turbidíticos en el Messiniense del Golfo de Valencia: una desecación imposible. *Rev. Soc. Geol. España*, 9: 97-116.
- Mein, P. (1975): Résultats du groupe de travail des vertébrés: biozonation du Néogène méditerranéen à partir des Mammifères. *Report Activity RCMNS working groups*, Bratislava: 78-81.
- Mein, P. (1990): Updating of MN zones. In: *European Neogene Mammal Chronology*. (E.H. Lindsay, V. Fahlbusch, and P. Mein, Eds.), Plenum Press, New York, *Nato ASI Ser.*, 180: 73-90.
- Michalzik, D. (1997): Sedimentary cycles in the Messinian Tertiary, Late Miocene, of SE Spain. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 203: 89-143.
- Pickford, M., Morales, J. and Soria, D. (1995): Fossil camels from the Upper Miocene of Europe: implications for Biogeography and faunal change. *Geobios*, 28: 641-650.
- Rosenzweig, M.L. (1975): On continental steady states of species diversity. In: *Ecology and Evolution of Communities* (M.L. Cody and J.M. Diamond, Eds.), Belknap Press, Cambridge, Massachusetts, 121-140.
- Rosenzweig, M.L. and Taylor, J.A. (1980): Speciation and diversity in Ordovician invertebrates: filling niches quickly and carefully. *Oikos*, 35: 236-243.
- Sala, B., Masini, F., Ficarelli, G., Rook, L. and Torre, D. (1992): Mammal dispersal events in the Middle and Late Pleistocene of Italy and Western Europe. *Cour. Forsch. Inst. Senckenberg*, 153: 59-68.
- Shackleton, M.J. (1984): Oxygen isotope evidence for Cenozoic climate change. In: *Fossils and Climate*. (P. Brenchley, Ed.), John Wiley, New York, pp. 27-34.
- Shackleton, N.J. 1995. New data in the Evolution of Pliocene Climatic Variability. In: *Paleoclimate and Evolution with Emphasis on Human Origins*. (E.S. Vrba, G.H. Denton, T.C. Partridge and L.H. Burckle, Eds.), Yale University Press, New Haven and London, 242-248.
- Shackleton, M.J. and Hall, M.A. (1984): Oxygen and carbon isotope stratigraphy of Deep Sea Drilling Project Hole 552A: Plio-Pleistocene glacial history. In: *Initial Reports of the Deep Sea Drilling Project*, 81 U.S. Government Print Off. (D.G. Robert, and D. Schnitker, Eds.), Washington, pp. 599-609.
- Steininger, F.F., Rabeder, G. and Rögl, F. (1985): Land Mammal Distribution in the Mediterranean Neogene: A Consequence of Geokinematic and Climatic Events. In: *Evolution of the Mediterranean Basin* (D.J. Stanley, and F.C. Wezel, Eds.), Raimondo Selli Commemoration, Springer Verlag, pp. 559-571.
- Stenseth, N.C. and Maynard Smith, J. (1985): Coevolution in ecosystems: Red Queen Evolution or stasis. *Evolution*, 38: 870-880.
- Stucky, R.K. (1990): Evolution of land mammal diversity in North America during the Cenozoic. *Curr. Mammal.*, 2: 375-432.
- Suc, J.-P., Bertini, A., Combourieu-Nebout, N., Diniz, F., Leroy, S., Russo-Ermolli, E., Zheng, Z., Bessais, E. and Ferrier, J. (1995): Structure of West Mediterranean vegetation and climate since 5.3 ma. *Acta zool. cracov.*, 38: 3-16.
- Torre, D., Ficarelli, G., Masini, F., Rook, L. and Sala, B. (1992): Mammal dispersal events in the Early Pleistocene of Western Europe. *Cour. Forsch. Inst. Senckenberg*, 153: 51-58.
- Van Valen, L. (1973): A new evolutionary law. *Evolut. Theory*, 1: 1-30.
- Vrba, E.S. (1985): Environment and evolution: alternative causes of the temporal distribution of evolutionary events. *South Afr. Jour. Sci.*, 81: 229-236.
- Vrba, E.S. (1995): On the Connections between Paleoclimate and Evolution. In: *Paleoclimate and Evolution with Emphasis on Human Origins*. (E.S. Vrba, G.H. Denton, T.C. Partridge and L.H. Burckle, Eds.), Yale University Press, pp. 24-45.
- Walker, T.D. and Valentine, J.W. (1984): Equilibrium models of Evolutionary Species diversity and the number of empty niches. *Amer. Natur.*, 124(6): 887-899.
- Webb, S.D. (1969): Extinction-origination equilibria in late Cenozoic land mammals of North America. *Evolution*, 23: 688-702.
- Williams, D.F., Thunell, R.C., Tappa, E., Rio, D. and Raffi, I. (1988): Chronology of the Pleistocene oxygen isotope record: 0-1.88 m.y. B.P. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 64: 221-240.

Manuscript received 27 May 1998

Accepted 7 March 1999