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Diversification and extinction patterns among Neogene perimediterranean mammals

By J.-J. Jaeger[1] and J.-L. Hartenberger[2]

[1] *Laboratoire de Paléontologie des Vertébrés, Université Pierre et Marie Curie (Paris VI) and C.N.R.S. URA* 720, 4 *Place Jussieu*, 75252 *Paris Cedex* 05, *France*

[2] *Institut des Sciences de l'Evolution, Université des Sciences et Techniques du Languedoc (Montpellier) and C.N.R.S. URA* 327, *Place E. Bataillon*, 34060 *Montpellier*, *France*

The best mammalian fossil record during the Neogene of Western Europe is that of the rodents, the most successful and diversified mammal order. The study of origination and extinction during the Neogene (24–3 Ma BP) in one of the best-documented areas, Spain and southern France, gives an insight into the dynamics of these communities and indicates the possible nature of the driving forces. Three main periods of time show a high rate of origination: the late Burdigalian (17.5 Ma BP), the early Vallesian (11.5–11 Ma BP) and the early Pliocene (4.2–3.8 Ma BP). Two of these high origination-rate periods are immediately followed by important extinction events during which all cohorts are deeply affected (11.5–11 Ma BP and 4.2–3.8 Ma BP). The most important extinction event seems to occur during the early Vallesian (11.5–11 Ma BP), which probably includes the middle/late Miocene boundary. At the Miocene/Pliocene boundary, and during the early Pliocene, the faunal turnover seems to become faster, inducing a strong decrease of the mean species duration. Whereas the main immigration event, which occurs at 17.5 Ma BP, can be related to other faunal migrations in terms of the closure of the Tethys, as it occurs also in eastern Africa and in southwest Asia, the middle/late Miocene boundary event may have been related to a period of ice growth in the Southern Hemisphere. The extinction event that affects the planktonic foraminifera at 12 Ma BP cannot be chronologically correlated to this southwestern European land-mammal extinction event, because the calibration of the marine fossil record during that time-span has to be precise. Some limited terrestrial faunal exchanges that occur during the Messinian between southwestern Europe and northwestern Africa do not deeply affect the general faunal dynamics. Both allochthonous cohorts of immigrants become rapidly extinct.

Several endemic rodent faunas, indicating insular conditions, have been reported from the southern edge of the western European continent from the middle Miocene up to the Pliocene. All show low taxonomic diversity, strong endemism and short survival. Some of them, like those of the Gargano Islands during the late Miocene, underwent peculiar morphological changes and also speciation. The large number of rodent genera coevolving in the Gargano Islands is indicative of the large surface areas of these islands. The general geographic pattern of southwestern Europe during the Neogene may therefore correspond to a large continental province including Spain and southern France with some kind of fast-modifying archipelago on its southern rim.

1. Introduction

During recent years, a large amount of data have been collected and analysed to relate the main biotic events to physical and geochemical changes. To understand the relations between the physical and biological worlds, two complementary points of view have arisen: some authors think that variation of the physical and chemical parameters of the various environments has immediate and important consequences in the development of life; others, mainly biologists, think that the evolutionary history of a species is largely dependent on other species, which constitute its most influential environment (Van Valen 1973; Stenseth & Maynard-Smith 1984; Hoffman & Kitchell 1984; Benton 1985). However, in this debate, most of the data that have been analysed originated from the marine realm, where physical and geochemical environmental parameters have been extensively studied in recent years. Indeed, most of the palaeobiological data relate to marine invertebrates and to protista. The evolutionary biology of these groups has not been extensively studied, so that the significance of their morphological changes, the species concept in each of these groups and their reproductive biology are not so fully understood as for higher organisms, such as mammals. For example, a mean species duration as estimated in Cainozoic planktonic foraminifera of about 25 Ma BP (Stanley 1979) and of 7.7 Ma BP for the upper half of the Cainozoic (Raup 1987) seems questionable relative to generation time among these groups. On the other hand, the known physical data relative to continental biotas are still incomplete.

In this context, we present here an analysis of the dynamic of mammalian faunas in a time interval of about 21 Ma, from the beginning of the Miocene to the end of the lowermost Pliocene, and in a restricted geographic area, around the Mediterranean.

2. METHODS

The fossil mammals of the perimediterranean area have been extensively studied since the time of G. Cuvier, some 180 years ago. A detailed survey indicates that at least one geographical area has been well documented, the southwestern part of Europe including Spain and southern France. Using the taxonomic results of different authors as a database, we have calculated several measures such as origination and extinction rates, duration of taxa and several classical derived parameters following the methods extensively used by authors such as Simpson (1944), Kurten (1960) and Stanley (1979).

The rodents are the most studied mammals in terms of their taxonomy and are represented, between the earliest Miocene and the late Early Pliocene, by 235 species distributed among 96 genera, giving an average of 2.52 species per genus. Large mammals are also numerous, but unlike the rodents, their taxonomy is still confusing and most of the families have not received comprehensive study in recent years. Therefore, after a preliminary and unsuccessful trial, we focused our study mainly on the rodents. Rodent taxonomy has reached some sort of consensus, having been recently established and verified independently by several research teams. Interest in rodent evolution is largely the result of their abundance in geological formations and of their biochronological value. This seems to be a consequence of their rapid diversification and phyletic evolution. The study of the dynamics of rodent faunas in southwestern Europe between 24 and 3 Ma BP therefore represents the main source of data from which the patterns have been deduced. The results obtained from the interpretation of these data will have to be tested in the future in the light of other faunal provinces and in other mammalian groups. However, the quality of that fossil record is several orders of magnitude higher than that of any other perimediterranean faunal province. Also the intrinsic value of the order Rodentia which, from the middle Paleogene on, represents half the diversity of herbivorous and omnivorous mammals, must also be considered. In this order the species concept used by palaeontologists has been shown to be rather close to the biological one. The reasons seem to be the qualities of high heritability of the dental characters used in taxonomy (Bader 1965), and the high adaptative value of teeth.

As the temporal scale is of major importance for the interpretation of the data, we have chosen the calibrated biochronological zonation proposed by Aguilar (1982), which appeared more detailed and more accurate than the classical land-mammal age zonation of Mein (1975). Also, as the biochronological unit is the marker level, its power of resolution is more accurate than the traditional land-mammal ages (Jaeger & Hartenberger 1975). The correlation between the continental timescale and the marine timescale is discussed by Aguilar & Michaux (1987). The recent timescale proposed by Vai (1988), which has improved the proposal of Berggren *et al.* (1985), has also been used. Taxonomic information has been collected in numerous recent works. We used mainly the papers of Aguilar (1981), Daams & Freudenthal (1981), Daams *et al.* (1987), Cuenca Bescos (1988) and Freudenthal (1988). Recent taxonomic publications of additional Spanish and French authors have also been used.

3. Genus duration

The histogram of the distribution of genus durations (figure 1*a*) has been constructed from extinct genera only. It is roughly similar to that obtained by Gingerich (1977) on several hundred genera of rodents with data collected from Romer (1966). Following a main peak of rather short survival time, there are several accessory peaks, situated respectively around 6–7, 10 and 21 Ma duration. Corresponding peaks are also observable on Gingerich's data. The genera corresponding to the 21 Ma peak belong to panchronic taxa, the living fossils of that period. The two other peaks characterize some genera that have an increased number of species, as shown on figure 3. The study of the distribution of species number relative to genus frequency illustrates a significative difference. There is no correlation between the genus duration and the number of species. The genera with short survival times have, in general, only a few species and their species number shows a logarithmic decrease. The genera with survival times longer than 5 Ma show a very different distribution, with a mode situated around three or four species. In that case, this pattern corresponds to a strategy, suggested by Raup (1987), in which the genera that speciate increase their chance of survival. But this cannot be considered as a general rule, as the longest-surviving genera of our study have only a few species, mainly chronospecies.

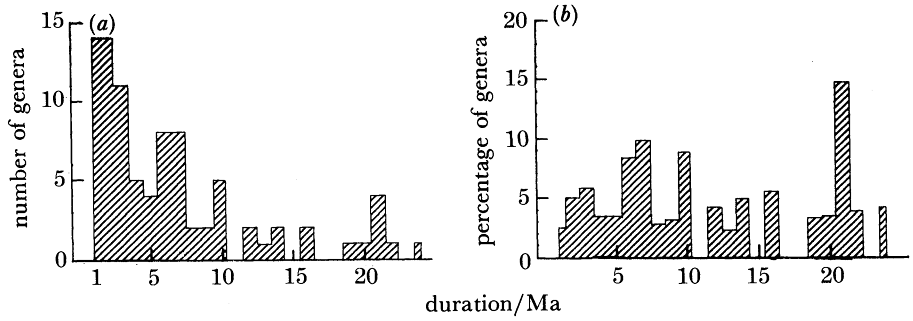

FIGURE 1. Generic duration of southwest European Neogene rodents. Only extinct genera have been plotted. (*a*) Histogram of longevities of genera of the interval. (*b*) Histogram of longevities of genera of an instant in time, following the method proposed by Stanley (1979, p. 110).

TABLE 1. RANGE CHART OF GENERA OF RODENTS IN THE NEOGENE OF SOUTHWESTERN EUROPE

(Correlation between marker levels, land-mammal ages and radiometric dating is made following information given in Berggren *et al.* (1985), Aguilar & Michaux (1987) and Vai (1988).)

Mein *et al.* zonation		0	1		2			3*a*		3*b*	4	5	6	7	8		9		10	11		12	13		14*a*	14*b*	15*a*	16*a*	16*b*	17		
Aguilar *et al.* zonation		A1	A1	A2	A3	A4	A4	A5	B1	B2	C1	C3	C4	C5	C5	D1	D2	D3	D4	D4	E	E	E	E	F1	F2	F3	G1	G2	G2	G3	
marker levels		Coderet	Plaissan	Paulhiac	Caunelles	Lespignan	Laugnac	Estrepouy	Serres de V.	Beaulieu	Vx Collonges	Sansan	Grive M	Grenatière	Anwill	Can Llobateres	Montredon	Mollon	Cucuron	Los Mansuetos	Lissieu	La Tour	Alcoy	Caravaca	Celleneuve	Hautimagne	Perpignan	Sète	Seynes	Balaruc	Iles Medas	recent
radiometric correlation		24	23.5	22.5	22	21	20	19.5	18.5	17.5	17	15.5	14	13	12.5	12	11	10.5	9	8.5	8	7	6	5.5	5	4.5	4	3.5	3	2.5	2	
Gliravus	←	●																														
Peridyromys	←	●	●	●	●	●	●	●	●	●																						
Microdyromys	←	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●																
Bransatoglis		●	●	●	●	●	●	●	●	●	●	●	●	●	●	●																
Glirudinus			●	●	●	●	●	●	●	●	●	●	●	●	●	●																
Pseudodryomys					●	●	●	●	●	●	●																					
Myoglis					●	●	●	●	●	●	●	●	●	●	●	●	●															
Vasseuromys							●																									
Altomiramys								●																								
Heteromyoxus							●																									
Miodyromys										●	●	●	●	●	●	●																
Eomuscardinus											●	●	●	●	●	●	●															
Muscardinus																●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●
Armantomys								●	●	●	●	●	●																			
Paraglirulus												●	●	●	●	●																
Miomymus																●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●
Tempestia													●																			
Glirulus																			●	●	●	●	●	●	●	●	●	●	●	●	●	●
Ramys																●																
Eliomys																●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●
Muscardinulus											●																					
Palaeosciurus	←	●	●	●	●	●	●	●	●	●	●																					
Heteroxerus	←	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●														
Spermophilinus									●	●	●	●	●	●	●	●	●	●	●	●												
Freudenthalia						●																										
Aragoxerus								●																								
Atlantoxerus											●	●	●	●																		
Petinomys										●	●	●	●	●	●	●	●	●	●	●	●	●	●	●								
Pliopetes																																
Pliopetaurista																		●	●	●	●	●	●	●	●	●	●					
Miopetaurista											●	●	●	●	●	●																
Blackia											●	●	●	●	●	●																
Cryptoterus											●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●						
Forsythia													●	●	●																	
Pliosciuropterus																																
Archaeomys	←	●	●																													
Issiodoromys	←	●																														
Allomys		●																														
Plesiominthus		●	●																													
Sminthozapus																									●							
Eozapus																					●											
Eomys	←	●	●	●	●	●	●	●	●	●	●																					
Eomyops													●	●	●	●	●	●	●	●	●											
Rhodanomys	←	●	●	●	●																											
Ritteneria						●																										
Ligerimys								●	●	●	●																					

TABLE 1 (*cont.*)

Mein *et al.* zonation		0	1		2			3*a*		3*b*	4	5	6	7	8		9		10	11		12	13		14*a*	14*b*	15*a*	16*a*	16*b*	17		
Aguilar *et al.* zonation		A1	A1	A2	A3	A4	A4	A5	B1	B2	C1	C3	C4	C5	C5	D1	D2	D3	D4	D4	E	E	E	E	F1	F2	F3	G1	G2	G2	G3	
marker levels		Coderet	Plaissan	Paulhiac	Caunelles	Lespignan	Laugnac	Estrepouy	Serres de V.	Beaulieu	Vx Collonges	Sansan	Grive M	Grenatière	Anwill	Can Llobateres	Montredon	Mollon	Cucuron	Los Mansuetos	Lissieu	La Tour	Alcoy	Caravaca	Celleneuve	Hautimagne	Perpignan	Sète	Seynes	Balaruc	Iles Medas	recent
radiometric correlation		24	23.5	22.5	22	21	20	19.5	18.5	17.5	17	15.5	14	13	12.5	12	11	10.5	9	8.5	8	7	6	5.5	5	4.5	4	3.5	3	2.5	2	
Pseudotheridomys	←	●	●	●	●	●	●	●																								
Keramidomys										●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●							
Eucricetodon	←	●	●	●	●	●	●	●	●																							
Pseudocricetodon	←	●	●	●	●																											
Adelomyarion	←	●																														
Melissiodon	←	●	●	●	●	●	●	●	●	●	●																					
Eumyarion										●	●	●	●	●	●	●																
Cricetodon										●	●	●	●	●	●																	
Megacricetodon										●	●	●	●	●	●	●																
Democricetodon										●	●	●	●	●	●	●	●	●														
Falbuschia										●	●																					
Lartetomys										●																						
Hispanomys												●	●	●	●	●	●	●	●	●	●											
Ruscinomys																			●	●	●	●	●	●	●	●	●	●				
Deperetomys													●	●	●																	
Cricetulodon																●	●	●	●	●												
Rotundomys																	●	●														
Kowalskia																		●	●	●	●											
Renzimys													●	●	●	●																
Cricetus																						●	●	●	●	●	●	●	●	●	●	●
Anomalomys											●	●	●	●	●	●	●	●														
Neocometes											●	●	●	●	●																	
Prospalax																									●							
Epimeriones																					●											
Cricetulus																														●	●	●
Myocricetodon																						●										
Progonomys																●	●	●														
Occitanomys																	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	
Parapodemus																		●	●	●	●											
Stephanomys																				●	●	●	●	●	●	●	●	●	●	●	●	●
Apodemus																						●	●	●	●	●	●	●	●	●	●	●
Rhagapodemus																						●	●	●	●	●	●	●	●	●		
Valerimys																		●	●	●	●	●	●	●	●	●	●	●	●	●		
Castillomys																									●	●	●	●	●	●	●	●
Micromys																											●	●	●	●	●	●
Paraethomys																					●	●	●	●	●	●	●	●	●			
‘Gerbillus’																									●							
Trilophomys																							●	●	●	●	●	●	●	●	●	●
Prosomys																											●					
Promimomys																																
Mimomys																												●	●	●	●	●
Rhizospalax		●	●																													
Monosaulax							●	●	●	●	●	●	●	●	●	●																
Steneofiber											●	●	●	●	●	●																
Castor																									●	●	●	●	●	●	●	●
Calomyscus																						●										
Dendromus																						●										
Protolophiomys																						●										
Hystrix																										●						

The commonest life history corresponds to an immigrant genus that becomes rapidly extinct after some unique speciation event.

Several methods allow us to evaluate the duration time of these genera. The arithmetic mean gives a value close to 7 Ma. The Lyellian curve (figure 2) indicates a half-life of 4 Ma, which would give a duration of 8 Ma with a coefficient of two as evaluated by Stanley (1979, p. 119) or a value of 11.5 Ma with a coefficient of 2.89 as demonstrated by Kurtén (1960) and Levinton & Farris (1987). On the other hand, the graphic method suggested by Stanley (1979) of constructing the histogram of genus duration for an instant of time, indicates two different modal values, one around 7 Ma, the other around 21 Ma (figure 1*b*). The last value characterizes the panchronic taxa, or living fossils. Gingerich (1977) has found an arithmetic mean of 5.85 Ma for all rodents.

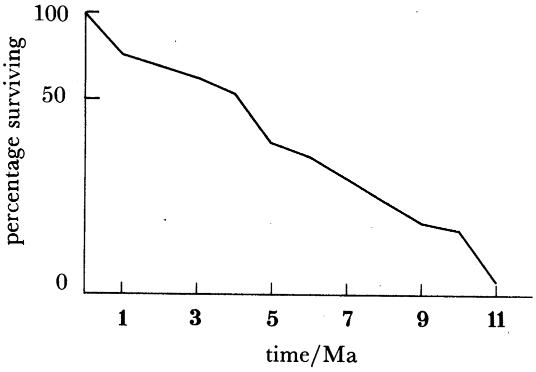

FIGURE 2. Partial (1 to 1 Ma) survivorship curve of genera of rodents of the southwest European Neogene. Only extinct genera have been plotted. Arithmetic mean 7.25; Lyellian mean 8.02 (*L*).

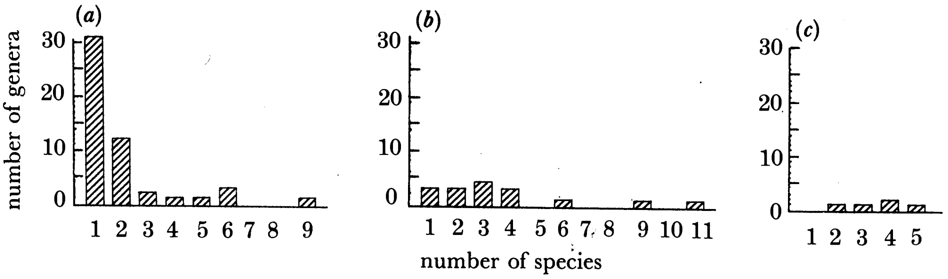

FIGURE 3. Histograms of species number (*a*) for genera with a duration of 0–5 Ma; (*b*) for genera with a duration of 5–10 Ma; and (*c*) for genera with a duration of 10–15 Ma.

Compared with histograms of genus duration for other taxa (Stanley 1979), the Neogene rodents of southwestern Europe show a logarithmic decrease of the genus number relative to their longevity. A similar pattern can also be observed when the duration of species is plotted (figure 4*a*). This shape may have some palaeobiological meaning, indicating that the palaeontological genus concept is close to the biological genus concept. These biological categories therefore behave in a similar way, but at different rates.

4. SPECIES DURATION

The histogram of species duration (figure 4*a*) indicates a distribution between 0.5 and 9 Ma, with a high proportion of species having a short survival time (64% survive less than 1 Ma).

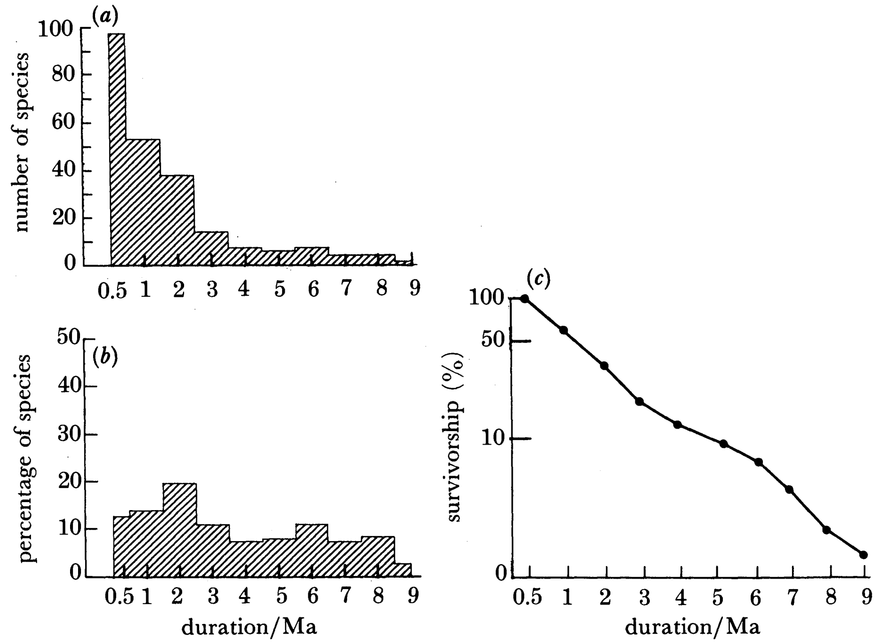

Figure 4. Species duration of southwest European neogene rodents. (*a*) Histogram of longevities of species of the interval; (*b*) histogram of longevities of species at an instant in time. (*c*) Survivorship curve of rodent species during the Neogene in southwestern Europe. Half of the species survived 1.25 Ma, corresponding to a Lyellian average of 2.5–3.60 Ma.

The general pattern appears to be quite similar to the histogram for graptolite species duration (figures 9 and 10 in Stanley 1979). The histogram of species duration for an instant of time (figure 4*b*) (Stanley 1979) indicates a modal duration of species of 2 Ma. On the Lyellian curve, a value of 1.25 Ma corresponds to the 50% ordinate (figure 4*c*). From different estimates, as for the genus, the mean species duration would have a value of 2.5 Ma as an underestimate or 3.6 Ma. Stanley (1979) indicates values of about 1.6 and 1.4 Ma for Pleistocene mammals, the last value becoming 2 Ma if the quotient of 2.89 is used (Kurtén 1960; Levinton & Farris 1987). For the Miocene rhizomyid rodents of southwest Asia, Flynn (1986) has recently observed an average value of 1.2 Ma. However, this author also gives an estimate of about 2.9 Ma for the smaller-sized species of rhizomyid.

To estimate more precisely the mean duration of species, we used a third method. For each polycohort (figure 8), we have constructed the survivorship curve for the rodent fauna of each zone through time. We measured mean species duration for each 'stratum' from the linear regression of each curve. As indicated by Raup (1987), if the value of the extinction rate is constant through time and from species to species in the cohort, the mean taxon duration must be the reciprocal of the extinction rate. We obtained a series of values between 2.4 and 0.16 Ma. When plotted against the absolute timescale (figure 5) the results suggest a decrease of the species duration during the Neogene.

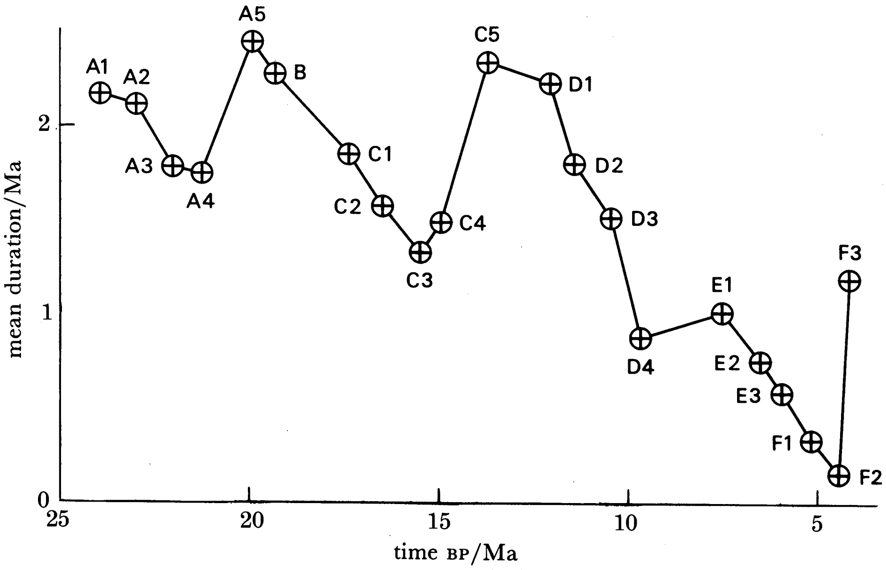

FIGURE 5. Mean average polycohort species duration through time (24–3 Ma BP). A decrease of polycohort species duration through time is observed.

5. ORIGINATION AND EXTINCTION RATES

(a) *Origination rates*

We have studied the origination rate at the generic level and at the specific level (figures 6 and 7) to appreciate the relative importance of phyletic evolution versus true immigration. Despite the possible origination of new genera through phyletic evolution, this event is much less frequent than the immigration of a new genus or the pseudo-origination of new species through gradual evolution. It should also be remembered that, as this work concerns only one faunal province, most of the immigration and extinction events may be local. Nevertheless, all modes of representation show a similar pattern. The global diversity follows a regular increase from the beginning of the Miocene up to the middle Miocene, followed by a regular decrease. Three major immigration events correspond respectively to the late Burdigalian (C1, 17.5 Ma BP), to the middle/late Miocene boundary (D1, 12 Ma BP) and to the early Pliocene. These immigration events have been recognized for a long time as basic chronostratigraphic events. Additional minor peaks can be observed, their amplitude depending on the mode of representation. Some are the result of immigrations: for example, the lower Vallesian (D1, 12 Ma BP) characterized by the appearance of *Hipparion* and of the earliest murid *Progonomys* (Schaub 1938) and the early Messinian (E1, 6.5 Ma BP) with a limited faunal exchange occurring between northwestern Africa and Spain. Other small peaks may be attributed to minor phases of faunal turnover.

(b) *Extinction rate*

Some important extinctions follow immediately after the main immigration phases. They can be explained as a simple return to faunal equilibrium following a strong increase of diversity as suggested by Gingerich (1977, 1984) for Pleistocene extinctions. The late Burdigalian extinction event (C1, 17.5 Ma BP) and the one that occurs during the late early Pliocene belong to this category.

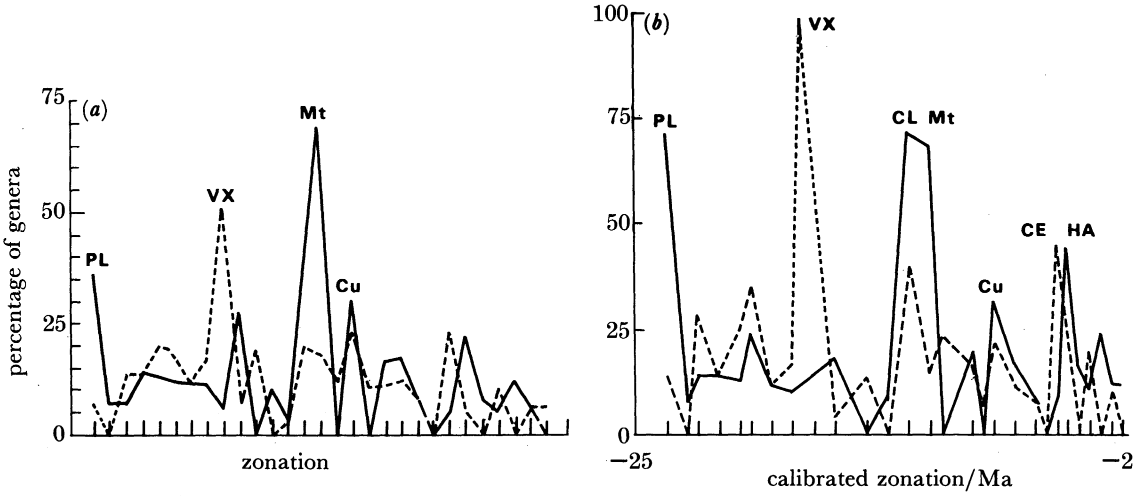

Figure 6. Variations of extinction (solid lines) and origination rates (dashed lines) of rodent genera through the Neogene of southwestern Europe. The timescale corresponds to the marker levels (*a*) and to the absolute timescale in Ma (*b*).

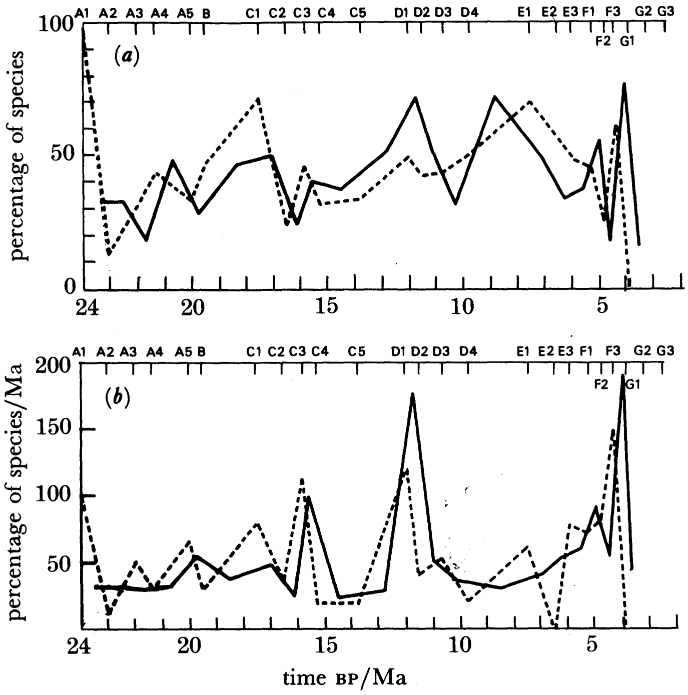

Figure 7. Variations of extinction (solid lines) and origination rates (dashed lines) of rodent species through the Neogene of southwestern Europe. (*a*) Percentage of the number of species represented in each zone. (*b*) Percentage of the number of species represented in each zone per million years.

The most important extinction event occurs during the early Vallesian (D1, 12–11.5 Ma BP). During this time interval, which most probably includes the middle/late Miocene boundary, the extinction rate reaches much larger values than the origination rate (figures 6 and 7). This period has been already recognized as a period of drastic changes in the composition of southwestern European mammal faunas (Crusafont Pairo 1954). Ecological scenarios have even been suggested for these changes (Weerd & Daams 1978; Daams & Van der Meulen

1984; Agusti *et al.* 1984) but the extinctions occurring during this timespan (around 0.5 Ma long) had not been suspected to be as important as that. As several large mammals disappear simultaneously (Moyà-Solà 1983), it can now be recognized as the major extinction event in the history of mammals during the Neogene of southwestern Europe. Its amplitude and taxonomic extent makes it very similar to the '*Grande Coupure*' event occurring at the Eocene–Oligocene boundary (Hartenberger 1987, 1988) in the same area. Unfortunately, the calibration of this event is not yet very accurate. It follows the immigration of *Hipparion* and of *Progonomys* into that area. On the basis of numerous observations, the immigration of *Hipparion* in the perimediterranean domain had been dated as 12.5 Ma BP by Berggren *et al.* (1985). However, recent data based on new K/Ar absolute ages and on magnetostratigraphic investigations (Sen 1986) suggest an earlier age of 11.5 or even 11 Ma BP. The Vallesian extinction event can therefore be estimated to date from 11 ± 0.5 Ma BP rather than 12–11.5 Ma BP, as in the timescale that we have used. This more accurate dating indicates that the middle/late Miocene boundary is probably included in the duration of that event. A similar major extinction has been reported among planktonic foraminifera at 12 Ma BP by Hoffman & Kitchell (1984). It has again been discussed by Raup (1987). Whether or not these two events, one occurring in the surface waters of the oceans and the other on land, are slightly diachronous or synchronous, cannot be decided yet as the timescale for the marine middle–late Miocene does not seem to be very accurately calibrated.

6. Polycohort and cohort survivorship curves

To analyse in greater detail the nature of these extinctions events, we have constructed polycohort (figure 8) and cohort (figure 9) species-survivorship curves similar to those constructed by Hoffman & Kitchell (1984) for Tertiary planktonic foraminifera, by Raup (1978, 1987) for Phanerozoic families of marine organisms and by Hartenberger (1987, 1988) for Palaeogene mammals of western Europe. These curves provide more precise information on the extinction patterns, because of the separate analysis of each faunal stratum. One of the most striking results is the similarity between the polycohort curves, showing all species occurring together at each successive level, and the cohort curves, which describe the extinctions occurring through time in each faunal stratum, each faunal stratum being restricted to the newly appearing species. This may indicate that the new species have an important weight in the determination of the shape of the polycohort curves.

The two strongest extinction events are those occurring during the early Vallesian (11 ± 0.5 Ma BP) and at the end of the early Pliocene (4.2–3.8 Ma BP) respectively. During these two crises, all curves are equally affected and show strong slopes. Other minor extinction events affect only the oldest faunal strata. This is so for the events that occur during C2 (16.5–15.7 Ma BP), the late Miocene (D3, 9 Ma BP) and immediately after the Miocene/Pliocene boundary (figures 5 and 6).

The general structure of these curves warrants some comments. In three zones (B, 19.5–17.5 Ma BP; C4, 15.3–13.8 Ma BP and E3, 6.5–5.2 Ma BP), the slopes of most of the polycohorts are nearly horizontal. The meaning of these patterns of slopes is not yet clear, as two interpretations can be proposed. First, they may correspond to a calibration error with the absolute timescale, the length of each of these zones having been overestimated. In that case, such errors would induce a kind of stepwise pattern indicative of a pseudo-stationary model

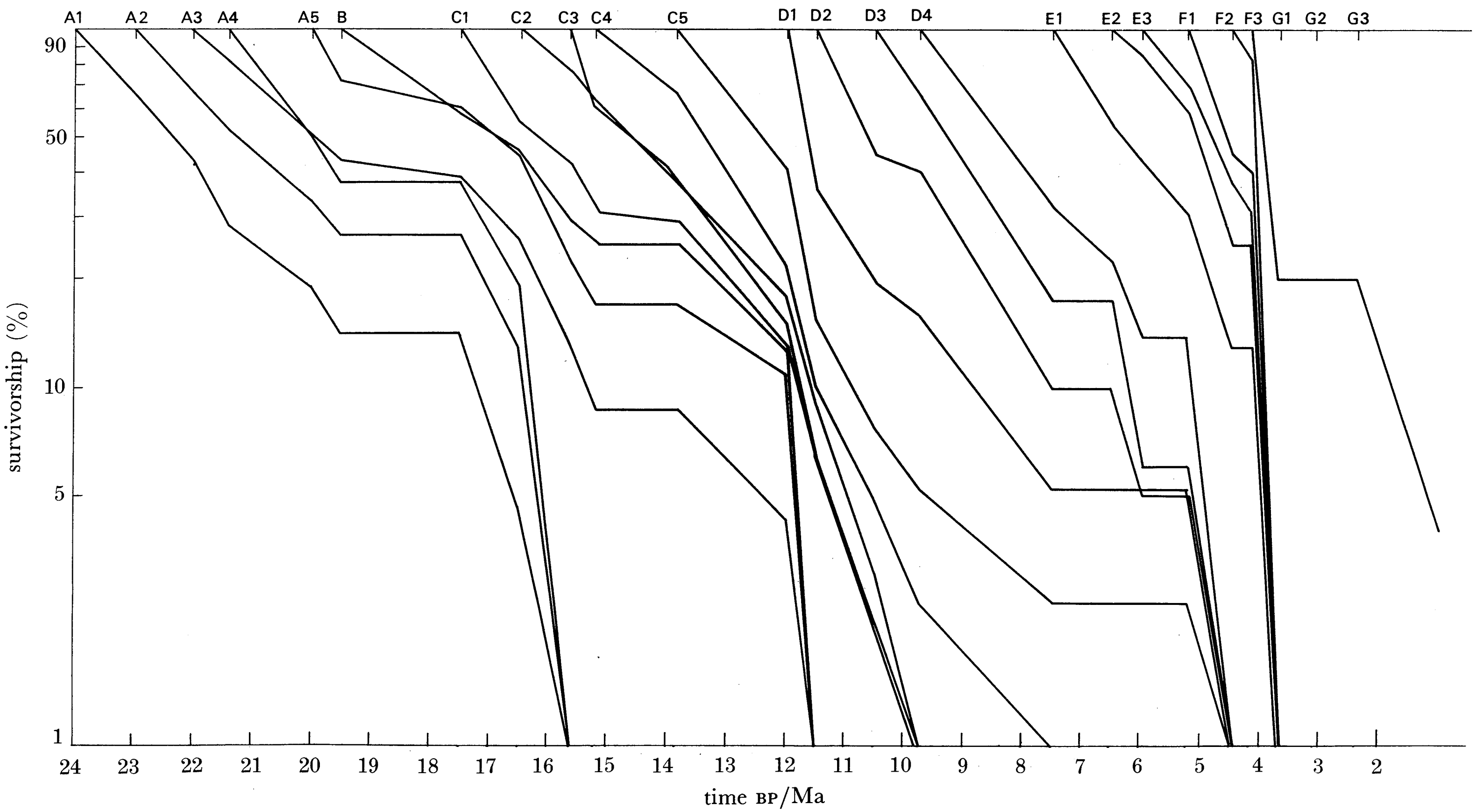

FIGURE 8. Nested polycohort survivorship curves of rodent species of the Neogene of southwestern Europe. The main extinction events occur during the D1–D2 interval (11.5–11 Ma BP) and the F3–G1 interval (4.2–3.8 Ma BP): all the cohorts are affected by these events. Minor events are recorded in C2 (16.5–15.7 Ma BP), in D3 (10.5–9.7 Ma BP) and in F1 (Lower Pliocene).

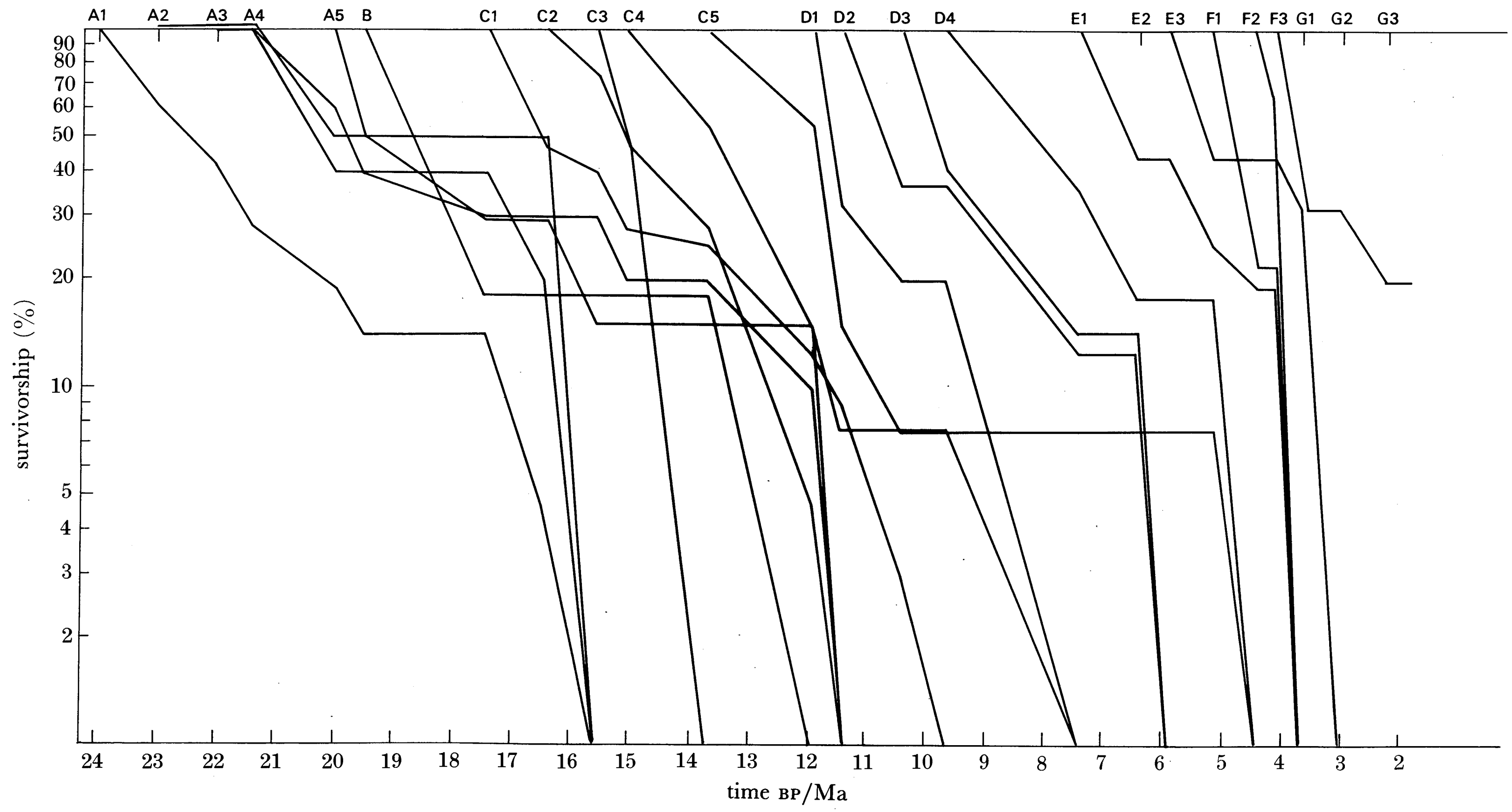

FIGURE 9. Nested true-cohorts survivorship curves of rodent species of the Neogene of southwestern Europe. The general pattern is close to that of figure 8.

(Stenseth & Maynard Smith 1984; Hoffman & Kitchell 1984). On the other hand, if the calibration can be demonstrated to be accurate for these periods, a stationary model, at least for some time intervals, will have to be accepted. However, the general shape of these curves is rather linear, supporting the Red Queen model (Van Valen 1973).

7. Relation with local and global changes

Despite some minor inadequacy in the calibration of our record, the correlations between the extinctions, the originations and the global changes can be discussed. The oceanic oxygen-isotope curve shows continuous increase of mean oceanic temperature from the early Miocene up to 15 Ma BP when a major and rapid decrease occurred. As for planktonic foraminifera (Hoffman & Kitchell 1984), our data do not show any kind of major change in the extinction rate during this drastic temperature drop. The only concomitant trend corresponds to an increase of diversity of rodent communities between 19 and 16 Ma BP followed by a sharp decrease between 16 and 12 Ma BP, which may be related to the temperature decrease indicated by the oceanic oxygen-isotope curve. Pickford (1987), on the basis of the East African mammalian fossil record, tentatively concluded that major shifts had occurred in biogeographic boundaries, inducing faunal exchanges between adjacent provinces, relating to the thermal optimum near 18 Ma BP (NDP1 in Thomas (1985)) and to the temperature decrease that occurs near 15 Ma BP (NDP2 in Thomas (1985)). The first of these changes is also represented in our record and corresponds to a main immigration phase (C1, 17.5 Ma BP) but we have found no indication relative to the second one in terms of origination and extinction rates, the main crisis in our record occurring around 11 Ma BP. Major faunal turnovers among the south Asiatic mammalian communities have been recognized between 20 and 16 Ma BP, at 9.5 Ma BP and at 7.4 Ma BP (Barry *et al.* 1985). The first of them, related to the closure of Tethys, corresponds to a major land-mammals exchange between Africa and Eurasia, reported all over the Old World.

In a recent oxygen-isotope synthesis, Miller *et al.* (1987) came to the conclusion that possible ice growth occurred near the middle/late Miocene boundary, for which they suggest an imprecise age of approximately 10–8 Ma BP. They explain the weaknesses of the chronological data as a consequence of the sparse North Atlantic record at these times and of a hiatus or lack of benthic data across this interval in the Indian Ocean record. Also, they relate their hypothesis to the occurrence of a major chronostratigraphic break and offlap events near the middle/late Miocene boundary, which have been suggested by Vail *et al.* (1977) and Haq *et al.* (1987), and with the occurrence of canyons incised into continental margins at this time (Farre 1985). Surprisingly however, Miller *et al.* (1987) indicate that no erosional event has been detected in the middle Miocene when a severe drop in temperature, deduced from oxygen-isotopic composition, occurs.

Some kind of global change seems therefore to be the cause of that main event affecting southwestern European mammalian faunas between 12 and 11 Ma BP, but its precise nature is not yet fully understood, most probably because of an imprecise marine chronological timescale that requires improvement.

The end of the Miocene and the beginning of the Pliocene appear to correspond, following our data, to a period of increased rate of faunal turnover long before the beginning of glacial ages in the North Atlantic region (Shackleton *et al.* 1984). Several immigrations are rapidly followed by extinctions. The mean species duration among the corresponding polycohorts is therefore especially short. We cannot yet relate these biological events to any other occurrences.

8. Faunal turnover in the adjacent areas

In adjacent areas, the fossil record of rodents is much less well documented than in southwestern Europe. In northwest Africa, the record begins only with the upper part of the middle Miocene (Lavocat 1961; Jaeger 1977). The number of taxa is always fewer than it is at corresponding time levels in southwestern Europe and large gaps still occur in the fossil record (Jaeger 1977). A high level of endemicity is shown if one compares these faunas with those of the adjacent geographic areas. During most of the documented timespan, only one or two genera of rodents, usually represented by different species, are shared with southwestern Europe, with the eastern Mediterranean province or with eastern Africa. This situation, and the low diversity, has led us to consider this faunal province as being isolated from adjacent areas. There is, however, one exception during the late Miocene, when a faunal exchange with southwestern Europe occurred (Brandy & Jaeger 1980; Thomas *et al.* 1982; Coiffait *et al.* 1985; Jaeger *et al.* 1987). Eight taxa, previously considered as endemic to an 'Ibero-Occitan' province, immigrated to North Africa where they became extinct through time (Jaeger *et al.* 1987).

Several occurrences of North African endemic taxa have also been reported from late Miocene Spanish localities (de Bruijn 1974; Jaeger *et al.* 1975; Aguilar *et al.* 1983; Moyà-Solà *et al.* 1984; Agusti & Galobart 1986; Aguilar & Thaler 1987). The resulting pattern of that faunal exchange is symmetrical to that observed in North Africa, with a progressive extinction of the African taxa. This kind of limited faunal exchange, not as yet clearly recognized on the basis of large mammals (Azzaroli & Guazzone 1980), occurred several times and at several places at the edge of the two different faunal provinces. The most important occurred during the late Miocene between Spain and northwest Africa, but it cannot be considered as being directly attributable to the desiccation of the western Mediterranean sea because it occurs a little earlier. A tectonic cause therefore seems more probable (Jaeger *et al.* 1987).

Several fossil islands have been identified during the Neogene, through the discovery of more or less endemic fossil mammals, and these relate to the complex tectonic story of the Mediterranean sea. From the early Middle Miocene of Sardinia, de Bruijn & Rümke (1974) have reported a peculiar micromammalian fauna with a mixture of African and European taxa. During the late Tortonian high sea-level stand, several islands occurred in the area that has since become Italy. The best-known is the one from Baccinello (Grosseto) in Tuscany, from which the hominoid *Oreopithecus bambolii* Gervais has been described. Extensive studies have led to an improved calibration of these deposits (Hürzeler 1975; Hürzeler & Engesser 1976) and to a better understanding of the biogeographic affinities of their faunas, which show strong African affinities (Hürzeler 1983; Thomas 1984). Faunas from successive levels have been discovered, indicating a very reduced number of species, an increasing endemicity and a fast rate of phyletic evolution. In the early Pliocene, the isolation ended, as testified by the arrival of a new fauna identical to the other western European early Pliocene faunas (Hürzeler & Engesser 1976). The dating of a volcanic-ash level, located above fossil endemic mammal localities, indicates an age of about 8 Ma BP (Hürzeler & Engesser 1976). The age of the beginning of the isolation, and its duration, are not yet established. From a palaeontological

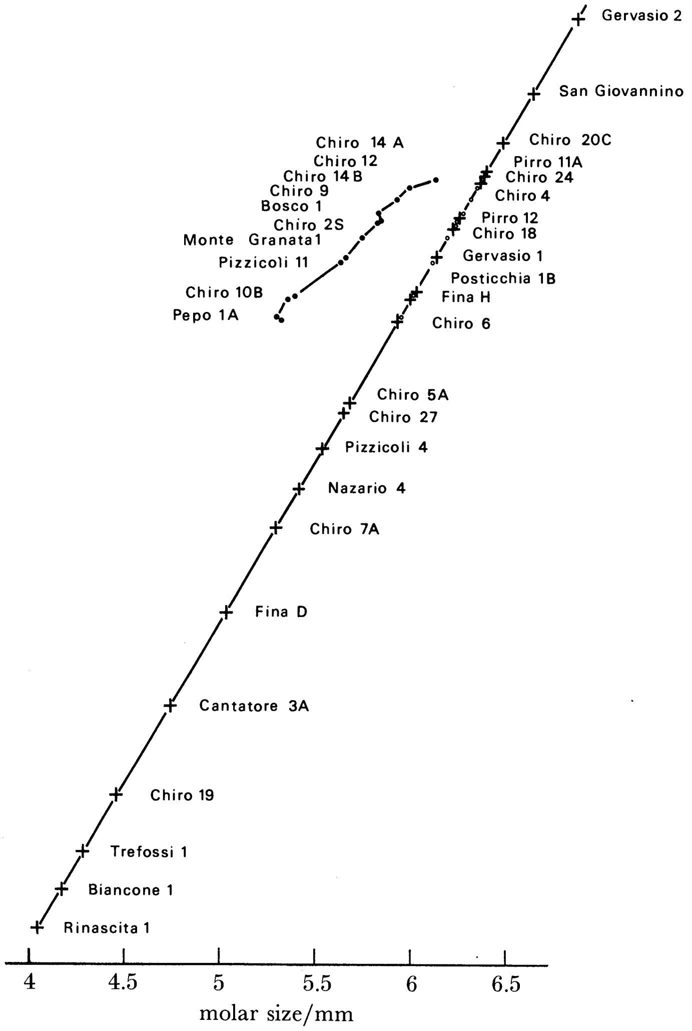

FIGURE 10. Relative position of the Gargano localities, using the increasing complexity of the molar structures and size of the murid *Microtia* as biochronological indexes (from Bastianelli 1989).

point of view, the beginning of the isolation must not have been before 10 Ma BP but a more recent age (8.5–9 Ma BP) cannot be excluded.

An even more spectacular example of island evolution occurring in the Mediterranean domain during the Neogene has been reported by Freudenthal (1971) from the Gargano area, in the province of Foggia, Italy. Numerous fossil mammal remains have been discovered in the '*terra rossa*' of a large number of karstic fissure fillings. The comparison of related taxa indicates that these fissure fillings were deposited during a notable timespan, especially when the amount of morphological changes occurring in various lineages is taken into account. From the available geological and palaeontological evidence, a late Miocene age has been proposed to include the whole sequence of localities (Freudenthal 1985), but an extension into the early Pliocene also cannot be excluded (De Giuli & Torre 1984). The fauna consists of numerous endemic taxa whose phylogenetic relationships are obscured because of their morphologically derived condition, a consequence of a rapid phyletic evolution following the beginning of their

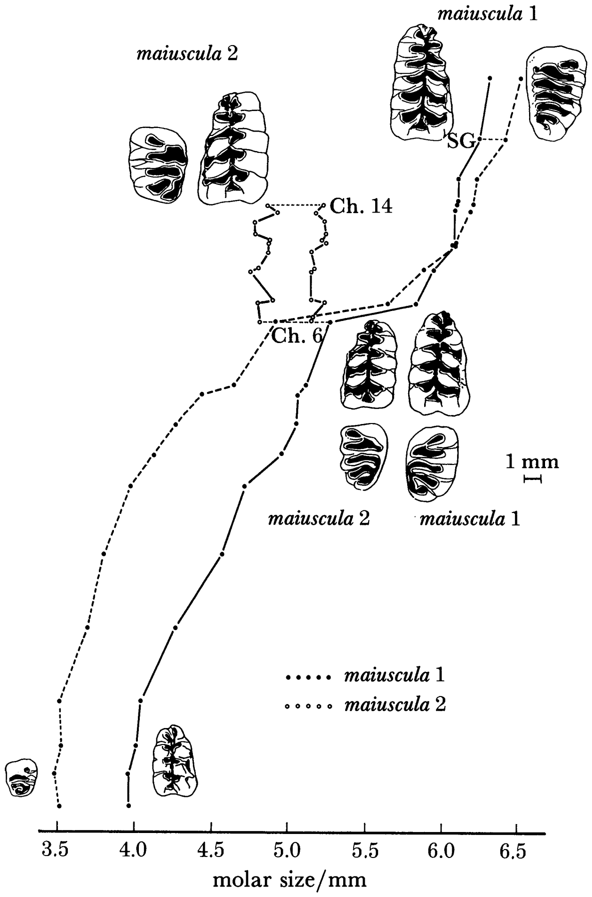

Figure 11. Morphological evolution of the largest species of *Microtia*, *M. maiuscula*, from the Gargano. At the level of Chiro 6 (Ch. 6), a second lineage appears, through sympatric speciation or through immigration from an adjacent island. After this event, there is a rapid increase of the morphological complexity in one lineage, whereas the size difference remains stable (from Bastianelli 1989).

isolation. Among them figure a cervid with five horncore-like cranial appendages (Leinders 1984), a giant erinaceid insectivore (Freudenthal 1972; Butler 1980), an unusually large owl (Ballmann 1973, 1976) and numerous endemic rodents (Daams & Freudenthal 1985), which deserve special attention. Until now, despite the fact that all material has not yet been fully investigated, nine rodent genera, distributed among three families (murids, cricetids and glirids), have already been identified with numerous species and chronospecies. Among them is the genus *Microtia*, a murid, members of which show an unusually large size associated with a peculiar molar morphology: the first lower molar shows an increased number of additional lobes in front of the tooth and the third upper molar also shows additional lobes in its distal part. These structures show a marked increasing complexity when the populations from different fissure fillings are compared. As there is no stratigraphic background, the relative age of each locality has been tentatively established by Freudenthal (1976) on the base of the supposed molar-size increase through time among several lineages of murids and cricetids. The alternative hypothesis of an increasing complexity of the molar structure through time as another measure of phyletic evolution, which can be combined with size, suggests a slightly different arrangement in the relative timescale (figure 10) (De Giuli & Torre 1984; Bastianelli

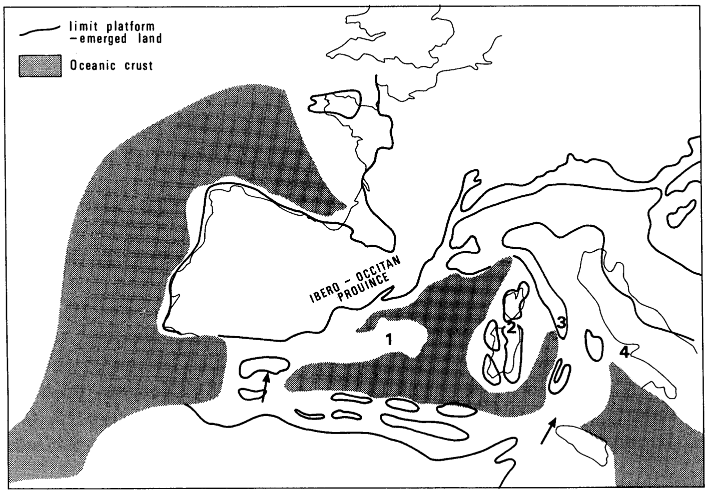

FIGURE 12. Palaeogeographical reconstruction of the Mediterranean during the Late Miocene (Tortonian), with indication of the main localities with endemic faunas. 1, Balearic Islands: 2, Sardinia; 3, Baccinello; 4, Gargano. Arrows indicate the main dispersal routes followed by terrestrial vertebrates.

1989) and allows the identification of several new lineages evolving simultaneously. As shown by Bastianelli (1989) (figure 11), the resulting pattern for the largest species of *Microtia* lineages indicates evidence of either sympatric speciation or immigration from an adjacent island. When compared with the limited number of fossil rodent species in the Pleistocene Mediterranean islands, the number of rodent taxa coevolving in these islands is rather high, suggesting that the area of these islands must have been very large (Diamond 1984). Unfortunately, their exact number and precise extension is largely unknown. Their area may have included a part of the area covered today by the Adriatic sea.

Other insular rodent faunas have also been discovered in the late Miocene of Ibiza (Balearic Islands) (Moyà-Solà *et al.* 1984) and in the early Pliocene of Sardinia (Pecorini *et al.* 1974).

In conclusion, the geography of the southern part of western Europe during Neogene time corresponded to a kind of archipelago, with many islands colonized by taxa originating from Europe or from northern Africa, related to the numerous tectonic, eustatic and climatic changes. In all these insular areas, the faunas underwent a rapid turnover and showed a high extinction rate, as can be expected among insular faunas. None of these numerous endemic taxa survived after the breakdown of the isolation, and the diversity, at least diversity that can be estimated on the base of the fossil record, seems to have been well related to the area of these islands (Diamond 1984). As more data are becoming available, the study of these insular faunas presents a stimulating subject with which to increase our knowledge of the driving forces that control the evolution of these communities. However, most if not all evolutionary novelties seem to have originated in larger faunal provinces where the driving forces seem to be more related to global events.

REFERENCES

Aguilar, J.-P. 1981 *Evolution des Rongeurs Miocènes et paléogéographie de la Méditerranée occidentale.* Ph.D. thesis, University of Montpellier.

Aguilar, J.-P. 1982 Biozonation du Miocène d'Europe occidentale à l'aide des Rongeurs et corrélations avec l'échelle stratigraphique marine. *C. r. Séanc. Acad. Sci., Paris* **294**, 49–54.

Aguilar, J.-P., Brandy, L. D. & Thaler, L. 1983 Les rongeurs de Salobrena (Sud de l'Espagne) et le problème de la migration messinienne. *Paléobiol. continent.* **14** (2), 3–17.

Aguilar, J.-P. & Michaux, J. 1987 Essai d'estimation du pouvoir séparateur de la méthode biostratigraphique des lignées évolutives chez les Rongeurs néogènes. *Bull. Soc. géol. Fr.* **8** (III), 1113–1124.

Aguilar, J.-P. & Thaler, L. 1987 *Protolophiomys ibericus* nov. gen., nov. sp. (Mammalia, Rodentia) du Miocène supérieur de Salobrena (Sud de l'Espagne). *C. r. Acad. Sci., Paris* **304**, 859–862.

Agusti, J., Moyà-Solà, S. & Gibert, J. 1984 Mammal distribution dynamics in the eastern margin of the Iberian peninsula during the Miocene. *Paléobiol. continent.* **14** (2), 33–46.

Agusti, J. & Galobart, A. 1986 La sucesion de micromamiferos en el complejo carstico de Casablanca (Almenara, Castellon): problematica biogeografica. *Paleontol. Evol.* **20**, 57–62.

Azzaroli, A. & Guazzone, G. 1980 Terrestrial mammals and land connections in the Mediterranean before and during the Messinian. *Palaeogeogr. Palaeoclimat. Palaeoecol.* **29**, 155–167.

Bader, R. S. 1965 Heritability of dental characters in the house mouse. *Evolution* **19**, 378–384.

Ballmann, P. 1973 Fossile Vögel aus dem Neogen der Halbinsel Gargano (Italien). *Scr. geol.* **17**, 1–75.

Ballmann, P. 1976 Fossile Vögel aus dem Neogen der Halbinsel Gargano (Italien), zweiter Teil. *Scr. geol.* **38**, 1–59.

Barry, J. C., Johnson, N. M., Mahmmood Raza, S. & Jacobs, L. L. 1985 Neogene mammalian faunal changes in Southern Asia: correlations with climatic, tectonic and eustatic events. *Geology* **13**, 637–640.

Bastianelli, S. 1989 Les *Microtia* (Rodentia, Muridae) du Gargano: de nouveaux résultats. *C. r. Acad. Sci., Paris.* (In the press.)

Benton, M. J. 1985 The Red Queen put to the test. *Nature, Lond.* **313**, 734–735.

Berggren, W. A., Kent, D. V., Flynn, J. & van Couvering, J. 1985 Cenozoic geochronology. *Bull. Am. Geol. Soc.* **96**, 1407–1418.

Brandy, L. D. & Jaeger, J.-J. 1980 Les échanges de faunes terrestres entre l'Europe et l'Afrique Nord-Occidentale au Messinien. *C. r. Séanc. Acad. Sci., Paris* **291**, 465–468.

de Bruijn, H. 1974 The Ruscinian rodent succession in Southern Spain and its implication for the biostratigraphic correlations of Europe and North Africa. *Senckenbergiana Lethaea* **55**, 435–443.

de Bruijn, H. & Rümke, C. G. 1974 On a peculiar mammalian association from the Miocene of Oschiri (Sardinia) I & II. *Proc. Konink. Nederland. Akad. van Wetensch.* B **77**, 46–79.

Butler, P. 1980 The giant erinaceid insectivore, *Deinogalerix* Freudenthal, from the upper Miocene of Gargano, Italy. *Scr. geol.* **57**, 1–72.

Coiffait, B., Coiffait, P. & Jaeger, J.-J. 1985 Découverte en Afrique du Nord des genres *Stephanomys* et *Castillomys* (Muridae) dans un nouveau gisement de microvertébrés néogènes d'Algérie orientale: Argoub Kemellal. *Proc. Konink. Nederland. Akad. van Wetensch.* B **88**, 167–183.

Crusafont Pairo, M. 1954 La zona pirenaica como filtro-barrera paleobiologico. *Inst. Est. Pirenaicos, Zaragoza*, pp. 317–332.

Cuenca Bescos, G. 1988 Revision de los Sciuridae del Aragoniense y del Rambliense en la fosa de Calatayud-Montalban. *Scr. geol.* **87**, 1–116.

Daams, R. & Freudenthal, M. 1981 Aragonian: the Stage concept versus Neogene Mammal Zones. *Scr. geol.* **62**, 1–17.

Daams, R. & Freudenthal, M. 1985 *Stertomys laticrestatus*, a new glirid (dormice, Rodentia) from the insular fauna of Gargano (Prov. of Foggia, Italy). *Scr. geol.* **77**, 21–27.

Daams, R., Freudenthal, M. & Sierra Alvarez, M. 1987 Ramblian; A new stage for continental deposits of early Miocene age. *Geol. Mijnbouw* **65**, 297–308.

Daams, R. & Van der Meulen, A. J. 1984 Palaeoenvironmental and palaeoclimatic interpretation of micromammal faunal successions in the Upper Oligocene and Miocene of North Central Spain. *Paléobiol. continent.* **14** (2), 241–258.

De Giuli, C. & Torre, D. 1984 Species interrelationships and evolution in the Pliocene endemic faunas of Apricena (Gargano peninsula, Italy). *Geobios, Mém. Spé.* **8**, 379–383.

Diamond, J. A. 1984 'Normal' extinctions of isolated populations. In *Extinctions* (ed. H. M. Nitecki), pp. 191–244. University of Chicago Press.

Farre, J. 1985 *The importance of mass wasting processes on the continental slope.* Ph.D. thesis, University of Columbia.

Flynn, L. J. 1986 Species longevity, stasis and stairsteps in Rhizomyid rodents. *Contributions to Geology, University of Wyoming, special paper* 3, pp. 273–285.

Freudenthal, M. 1971 Neogene vertebrates from the Gargano peninsula, Italy. *Scr. geol.* **3**, 1–10.

Freudenthal, M. 1972 *Deinogalerix koenigswaldi* nov. gen., nov. sp., a giant insectivore from the Neogene of Italy. *Scr. geol.* **14**, 1–19.

Freudenthal, M. 1976 Rodent stratigraphy of some Miocene fissure fillings in Gargano (prov. Foggia, Italy). *Scr. geol.* **37**, 1–18.

Freudenthal, M. 1985 Cricetidae (Rodentia) from the Neogene of Gargano (Prov. of Foggia, Italy). *Scr. geol.* **77**, 29–76.

Freudenthal, M. (ed.) 1988 Biostratigraphy and paleoecology of the Neogene micromammalian faunas from the Calatayud–Teruel Basin (Spain). *Scr. geol.* (Special issue 1.)

Gervais, P. 1872 Sur un singe fossile, d'espèce non encore décrite, qui a été découvert au Monte Bamboli. *C. r. hebd. Séanc. Acad. Sci., Paris* **74**, 1217.

Gingerich, P. D. 1977 Patterns of evolution in the mammalian fossil record. In *Patterns of evolution* (ed. A. Hallam), pp. 469–500. Amsterdam: Elsevier.

Gingerich, P. D. 1984 Pleistocene extinctions in the context of origination-extinction equilibria in cenozoic mammals. In *Quaternary extinctions: a prehistoric revolution* (ed. P. S. Martin & R. G. Klein), pp. 211–222. Tucson: University of Arizona Press.

Haq, B. U., Hardenbol, J. & Vail, P. R. 1987 Chronology of fluctuating sea levels since the Triassic. *Science, Wash.* **235**, 1156–1167.

Hartenberger, J.-L. 1987 Modalités des extinctions et apparitions chez les mammifères du Paléogène d'Europe. *Mém. Soc. géol. Fr.* **150**, 133–143.

Hartenberger, J.-L. 1988 Etudes sur la longévité des genres de Mammifères fossiles du Paléogène d'Europe. *C. r. Acad. Sci., Paris* **306**, 1197–1204.

Hoffman, A. & Kitchell, J. A. 1984 Evolution in a pelagic planktic system: a paleobiologic test of multispecies evolution. *Paleobiology* **10**, 9–33.

Hürzeler, J. 1975 L'âge géologique et les rapports géographiques de la faune de mammifères du lignite de Grosseto. In *Problèmes actuels de paléontologie. Evolution des vertébrés*, pp. 873–876. Paris: Coll. intern. CNRS number 218.

Hürzeler, J. & Engesser, B. 1976 Les faunes de mammifères néogènes du bassin de Baccinello (Grosseto, Italie). *C. r. hebd. Séanc. Acad. Sci., Paris* **283**, 333–336.

Hürzeler, J. 1983 Un alcelaphiné aberrant (Bovidé, Mammalia) des 'lignites de Grosseto' en Toscane. *C. r. Séanc. Acad. Sci., Paris* **296**, 497–503.

Jaeger, J.-J. & Hartenberger, J.-L. 1975 Pour l'utilisation systématique de niveaux-repères en biochronologie mammalienne. In *R.A.S.T.* (ed. Soc. géol. France), p. 201. Paris.

Jaeger, J.-J., Michaux, J. & Thaler, L. 1975 Présence d'un rongeur Muridé nouveau, *Paraethomys miocaenicus* nov. sp. dans le Turolien supérieur du Maroc et d'Espagne. Implications paléogéographiques. *C. r. hebd. Séanc. Acad. Sci., Paris* **280**, 1673–1676.

Jaeger, J.-J. 1977 Les rongeurs du Miocène moyen et supérieur du Maghreb. *Palaeovertebrata, Montpellier* **8**, 1–166.

Jaeger, J.-J., Coiffait, B., Tong, H. & Denys, C. 1987 Rodent extinctions following Messinian faunal exchanges between Western Europe and Northern Africa. *Mém. Soc. géol. Fr.* **150**, 153–158.

Kurtén, B. 1960 Chronology and faunal evolution of the earlier European glaciations. *Soc. scient. Fenn. Comm. Biol.* **21**, 40–62.

Lavocat, R. 1961 Etude systématique de la faune de mammifères et conclusions générales. In *Le gisement à vertébrés miocènes de Beni-Mellal (Maroc). Notes Mém. Serv. Mines Carte géol. Maroc* **155**, 9–11, 29–94, 109–142.

Leinders, J. 1984 Hoplitomerycidae fam. nov. (Ruminantia, Mammalia) from Neogene fissure fillings in Gargano (Italy). Part 1: The cranial osteology of *Hoplitomeryx* gen. nov. and a discussion on the classification of pecoran families. *Scr. geol.* **70**, 1–51.

Levinton, J. S. & Farris, J. S. 1987 On the estimation of taxonomic longevity from Lyellian curves. *Paleobiology* **13**, 479–483.

Mein, P. 1975 Biozonation du Néogène méditerranéen à partir des Mammifères. In *Report on activity of the R.C.M.N.S. working group*, pp. 78–81. Bratislava.

Miller, K. G., Fairbanks, R. G. & Mountain, G. S. 1987 Tertiary oxygen isotope synthesis, sea level history and continental margin erosion. *Palaeoceanography* **2**, 1–19.

Moyà-Solà, S. 1983 Los boselaphini (Bovidae, Mammalia) del Néogeno de la Peninsula Iberica. Ph.D. Thesis, University of Barcelona.

Moyà-Solà, S., Agusti, J. & Pons-Moyà, J. 1984 The Mio-Pliocene insular faunas from the West Mediterranean origin and distribution factors. *Paléobiol. continent.* **14** (2), 347–357.

Pecorini, G., Rage, J.-C. & Thaler, L. 1974 La formation continentale de Capo Mannu, sa faune de vertébrés pliocène et la question du Messinien de Sardaigne. *Rc. Semin. Fac. Sci. Univ. Cagliari*, **13** (Suppl.), 302–319.

Pickford, M. 1987 Concordance entre la paléontologie continentale de l'Est africain et les événements paléo-océanographiques au Néogène. *C. r. Acad. Sci., Paris* **304**, 675–678.

Raup, D. M. 1978 Cohort analysis of generic survivorship. *Paleobiology* **2**, 289–297.

Raup, D. M. 1987 Major features of the fossil record and their implications for evolutionary rate studies. In *Rates of evolution* (ed. Campbell, K. S. W. & Day, M. F.), 1–14.

Romer, A. S. 1966 *Vertebrate paleontology*. University of Chicago Press.

Schaub, S. 1938 Tertiäre und Quartäre Murinae. *Abh. Schweiz. Pal. ges.* **45**, 1–39.

Sen, S. 1986 Contributions à la magnétostratigraphie et à la Paléontologie des formations continentales néogènes du pourtour Méditerranéen. Implications biochronologiques et paléobiologiques. Ph.D. Thesis, University Pierre et Marie Curie, Paris.

Shackleton, N. *et al.* 1984 Oxygen isotope calibration of the onset of ice rafting and history of glaciation in the North Atlantic region. *Nature, Lond.* **307**, 620–623.

Simpson, G. G. 1944 Tempo and mode in evolution. New Haven, Connecticut: Yale University Press.

Stanley, S. M. 1979 *Macroevolution pattern and process*. San Francisco, California: Freeman.

Stenseth, N. C. & Maynard-Smith, J. 1984 Coevolution in ecosystems: Red Queen or stasis. *Evolution* **38**, 870–880.

Thomas, H. 1984 Les origines africaines des Bovidae (Artiodactyla, Mammalia) miocènes des lignites de Grosseto (Toscane, Italie). *Bull. Mus. natn. Hist. nat., Paris* **6**, 81–101.

Thomas, H. 1985 The early and middle Miocene land connection of the Afro-Arabian and Asia: a major event for the Hominoid dispersal. In *Ancestors: the hard evidence* (ed. E. Delson), pp. 42–50. New York: A. R. Liss.

Thomas, H., Bernor, R. & Jaeger, J.-J. 1982 Origines du peuplement mammalien en Afrique du Nord pendand le Miocène terminal. *Géobios* **15** (3), 283–297.

Vai, G. B. 1988 A field guide to the Romagna Apennine geology: the Lamone valley. In *Fossil vertebrates in the Lamone valley* (ed. C. De Giuli & G. B. Vai), pp. 7–37. Faenza: Università di Bologna.

Vail, P. R., Mitchum, R. M. Jr & Thompson, S. 1977 Seismic stratigraphy of global changes of sea-level. Part 4: Seismic stratigraphy. Applications to hydrocarbon exploration. *Mem. Am. Ass. petroleum Geol.* **26**, 83–96.

Van Valen, L. 1973 A new evolutionary law. *Evol. Theory* **1**, 1–30.

van de Weerd, A. & Daams, R. 1978 Quantitative composition of rodent faunas in the Spanish Neogene and palaeoecological implications. *Proc. Konink. Nederland. Akad. van Wetensch.* B **81**, 448–473.