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Biogeography of circum-Mediterranean Miocene–Pliocene rodents; a revision using factor analysis and parsimony analysis of endemicity

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Abstract

The biogeographic relationships of North African Miocene–Pliocene rodent faunas are assessed using two different methods, factor analysis and parsimony analysis of endemicity. The Mediterranean basin is a true biogeographic province. Within it, North Africa makes up a sub-province of its own, only slightly closer to the Ibero-Occitanian sub-province than to the eastern Mediterranean one. These three sub-provinces retain their permanency over time, localities within them being clustered according to their geological age rather than by geographic location. The Miocene–Pliocene is a period of strong, but transitory similarity between the north and south, while there is a steady trend toward homogenisation of the northern Mediterranean. Most of the exchanges occur, through France, between the eastern Mediterranean and eastern Spain, and between the latter area and the rest of Iberia and North Africa, while there are very few trans-Mediterranean and southern longitudinal exchanges. © 1998 Elsevier Science B.V.

Keywords: Rodents; Miocene; Pliocene; Mediterranean region; Biogeography; North Africa

1. Introduction

The biogeographic relationships of North African mammalian faunas during the late Neogene have been a matter of controversy for some time (see e.g. Forsten, 1978; Thomas, 1979, 1984; Thomas et al., 1982; Geraads, 1982; Bernor and Pavlakis, 1987). Usually, this topic has been discussed in terms of exchanges of specific taxa, rather than of overall similarity of assemblages. A notable exception is Agustí (1989) who explained similarities between Spain and North Africa by fluctuation of the boundaries between biogeographic areas. Today, the Maghreb, north of the Sahara, is often included in a Mediterranean province, but the very existence of this province has been debated (see references in Aulagnier, 1992).

Present-day large mammals and bats are of palearctic affinities (Kowalski and Rzebik-Kowalska, 1991), but this results largely from Late Pleistocene extinction of Ethiopian elements, partly correlated with immigration of northern taxa (Geraads, 1982). A similar replacement pattern may be valid for other groups of Vertebrates, such as freshwater fish (Greenwood, 1973; Gaudant, 1987). Yet, almost nothing is

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known of late Neogene birds and reptiles in this area. It might be expected that much of the present-day mammalian biogeography of North Africa, at the border between two major areas, could be explained by historical factors in late Neogene times, with the Messinian crisis ranking first among them. Unfortunately, very few large mammal faunas are known in North Africa near the Miocene–Pliocene boundary. The only rich one is the Upper Miocene locality of Sahabi (Boaz et al., 1987). Most of its mammals are of African type, with only a few northern elements (such as the Bovid *Prostrepsiceros*).

Micromammal localities are far more common, and rodents are easier to identify. Present-day rodents of the Maghreb are mostly of Ethiopian and Saharo-Sindian affinities (Aulagnier, 1992); only *Apodemus* and *Eliomys* have never been recorded from the Ethiopian realm. Fossil faunas are usually seen as reflecting endemism, with several long-lasting lineages, but also document several phases of faunal exchange with the North (mainly Spain) during Late Miocene times (Brandy and Jaeger, 1980; Coiffait-Martin, 1991). However, choice of biogeographic scenarios, and especially of the direction of the migrations, depends upon the quality of the fossil record. This to the extent that almost every new fossil locality seems to provide evidence of a new exchange phase. For instance, the new site of Lissasfa, near Casablanca, Morocco (Geraads, 1997) has yielded a hypsodont cricetid similar to the European *Ruscinomys*, but more primitive than all species of this genus by its little reduced third molars, as in the eastern Mediterranean *Byzantinia*. Thus, it could be an evolved offshoot of the latter, immigrated into North Africa. These alternative identifications would of course imply very different migration routes or vicariant events at different periods. Therefore, rather than relying on a small number of taxa and trying to assess their biogeographic history, I have chosen to compare a large number of faunas from the whole Mediterranean area. The results achieved using these methods are little affected by incompleteness of documentation, or by incorrect identifications. They therefore provide a sound basis for biogeographic interpretations, even though they do not always give answers concerning centres of origin or migration routes.

2. Data

2.1. Localities

A total of 89 localities were used. The assemblages come from stratified and fissure deposits. They belong mainly to the Late Miocene and Early Pliocene (MN 13 and MN 14 of European mammalian nomenclature), but some of them are as old as early Turolian or as late as early 'Villafranchian'. Although not laying claim to completeness, this list includes the bulk of important non-insular micromammal sites of the Miocene–Pliocene transition in the Mediterranean area. Almost half of them are from eastern and central Spain, which are by far the richest areas. I have not included central European localities, which are, a priori, more distant from North Africa and the incorporation of which would have enlarged the sample unnecessarily. In 'sub-Saharan' Africa, micromammal localities of the Miocene–Pliocene boundary interval are extremely rare. I have only included three Pliocene sites of East Africa and two in South Africa. There are also a few localities in Asia, most of which are concentrated in the eastern Mediterranean.

2.2. Taxa

All Rodent taxa present in at least one of the localities were included in any given analysis. Most taxa are used at the generic level, but some of the most frequent (and best studied) ones are also used at the specific level: *Apodemus*, *Cricetus*, *Eliomys*, *Occitanomys*, *Paraethomys*, *Ruscinomys*, *Stephanomys*; for instance, *Eliomys truci* is entered both as *Eliomys* and as *E. truci*. A similarity at the specific level is therefore more significant than at the generic level only. This is of course a non-demonstrable assumption, but it is impossible to weigh all taxa a priori according to their potential significance. A few other taxa, rare and usually not precisely identified, were only included at the family level: Castoridae, Hystricidae, Lophiomyidae, Spalacidae, Thryonomyidae.

I have always tried to use the most recent or more consensual determinations, but it is clear that not everyone will fully agree with the data presented in Appendix A. In any case, minor changes in the faunal lists do not seriously alter the overall pattern. This is convincingly shown, for instance, by entering alternative determinations for the hypsodont cricetid of North Africa.

3. Factor analysis

Correspondence factor analyses have been performed (using software SPAD-N©, CISIA, Paris) on the data matrix of localities × presence/absence of taxa. The first analysis has been conducted on all 89 localities and 131 taxa. The data are poorly structured, since the first two axes account for only 14% of the variance and the first four axes for 25%, but this is of course not unexpected, given the great number of variables. For instance, Denys (1990, p. 360) gave the value of 35% for four axes, for a data set more than four times smaller and much more homogeneous biogeographically. The general pattern, however, is quite clear: the French, Spanish and eastern Mediterranean localities are closely clustered. Those in North Africa are somewhat apart, while the remaining African and Asiatic localities plot much farther. However, the relative distances from North Africa to East and South Africa are roughly those predicted by geography, and there is, thus, no need for a Saharan barrier at that time period. On the whole, there is a good agreement between geographic situation and position in space 1–3, except perhaps that eastern and western Mediterranean are closer than expected, suggesting similar climate and environment (Fig. 1). The most obvious result, is that the main factor controlling resemblance is geography, not chronology. Localities cluster according to their location, even though they span several MN zones. For instance, the two Siwalik sites are close to each other, despite a difference in age of about 2 m.y. All Moghrebian sites are also grouped. This is still more true of the Spanish sites, even though they range in age from early Turolian to mid-Pliocene.

The second clear result is that the whole Mediterranean basin, including France, the Iberian peninsula, North Africa, Greece and Turkey, forms a homogeneous unit, quite isolated from Asia and from East and South Africa. Thus, the existence of a Mediterranean micromammal province in the Miocene–Pliocene is not in doubt. The area which is closest to most North African localities is Spain, as could have been expected, but the eastern Mediterranean is not much farther off. It follows that the impact of the climatic and palaeogeographic events at that time should not be evaluated only in terms of north–south exchanges, but longitudinally as well.

The Mediterranean basin being obviously homogeneous, a second analysis has been conducted on its 79 localities, with 86 variables, to evaluate relationships within this area more precisely. A very clear picture emerges from this analysis. All European and eastern Mediterranean localities are aligned along a line more or less parallel to axis 3, almost perpendicular to plane 1–2 (Figs. 2 and 3). The main factor controlling their position along axis 3 is age, with older localities having higher positions, but this is mainly true of the Greek and Turkish sites, of which only the most recent ones approach the Spanish localities, and these are all closely clustered. Specificity of the eastern Mediterranean in respect to western Europe decreases with time. This could be the last phase of a trend which began in the Early Miocene (De Bruijn, pers. commun.). North African localities are arranged in a crescent fashion, independently from the northern and eastern group of sites. The main factor responsible for the position within this crescent is also age, which changes along axes 2 and 3, Sidi Salem (early Turolian) being at one end, Aïn Brimba (Middle Pliocene?) at the other. This distribution is quite clear and could perhaps even give suggestions about the dating of some localities of uncertain age (e.g., Sahabi is perhaps even earlier than Late Miocene, or its fauna could be a mixture from different levels). Near its mid-length, the North African crescent approaches the line of northern and eastern sites, thereby visualising the phase of greatest similarity. North African

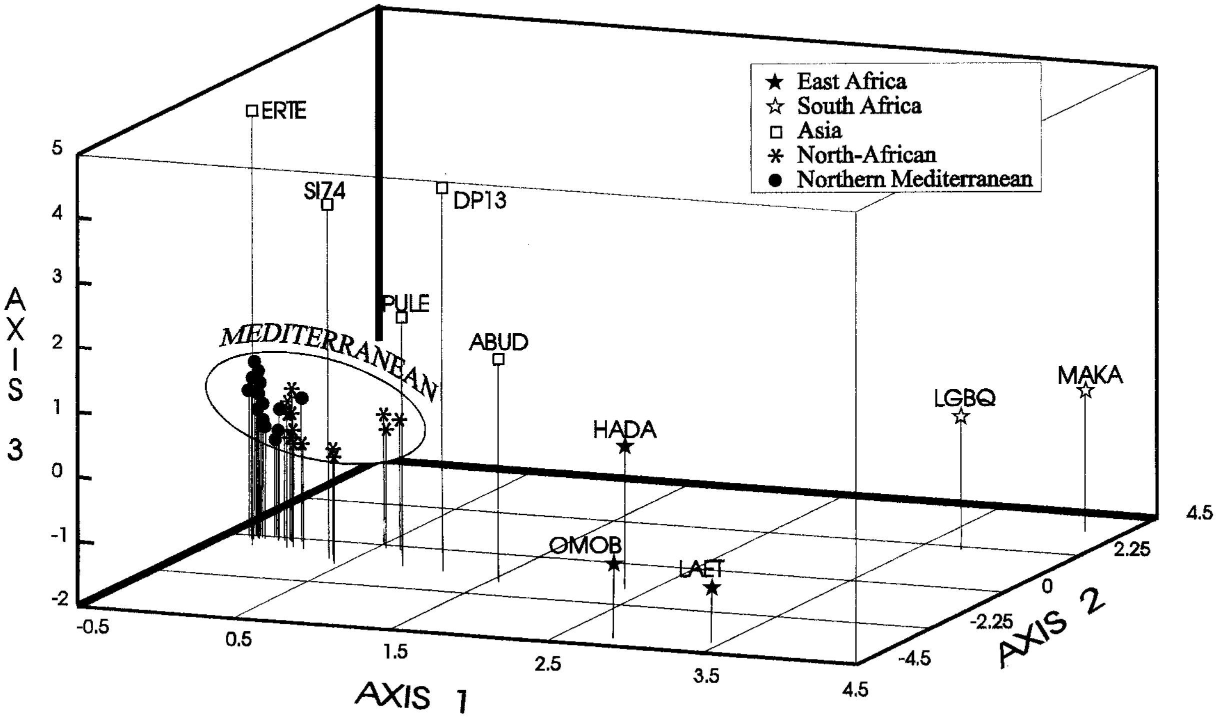

Fig. 1. Position of the localities in space 1–2–3 of the first analysis. Eigenvalues: axis 1, 0.89 (7.76%); axis 2, 0.69 (6.05%); axis 3, 0.66 (5.75%). See Appendix A for abbreviations.

sites closest to this tangential point date from the Late Miocene; only one of them, Aïn Guettara, becomes included in the non-African group, and it is clearly, as stated by its discoverers (Brandy and Jaeger, 1980) the North African site most similar to the Spanish ones. However, the closeness of some other North African and Spanish sites shows that this is not just a sudden phenomenon, but the result of a general trend already initiated in middle 'Turolian' times, North African sites like Khendek el Ouaich, Beni Brahim and Argoub Kemellal being only slightly less 'Spanish like'. This trend reaches its climax at the Miocene–Pliocene boundary. The age and duration of this exchange phase shows that it is not strictly linked to the Messinian crisis (Benammi et al., 1996). After that, North Africa diverges again from Spain, mainly because of the arrival of *Mus* in the former area and of local extinctions (Jaeger et al., 1987).

4. Biogeographic provinces

Single taxa are often used to define biogeographic provinces, but with regards to rodents, which are very sensitive to ecological conditions, the distribution of any one of them does not allow more than the recognition of its own realm. Taking whole faunas into consideration allows the recognition of areas of greater similarity, which are less likely to have a purely ecological significance.

A tree can be constructed from the co-ordinates of the localities, using Ward's hierarchical grouping method, which minimises decrease of variance at each aggregation (Ward, 1963; Sneath and Sokal, 1973, p. 241). For the Mediterranean sites; I have used the first 36 axes, which are needed to account for 90% of the variance. This allows of course an easier and more complete visualisation of the relationships between localities. This tree can then be parted into clusters of more similar

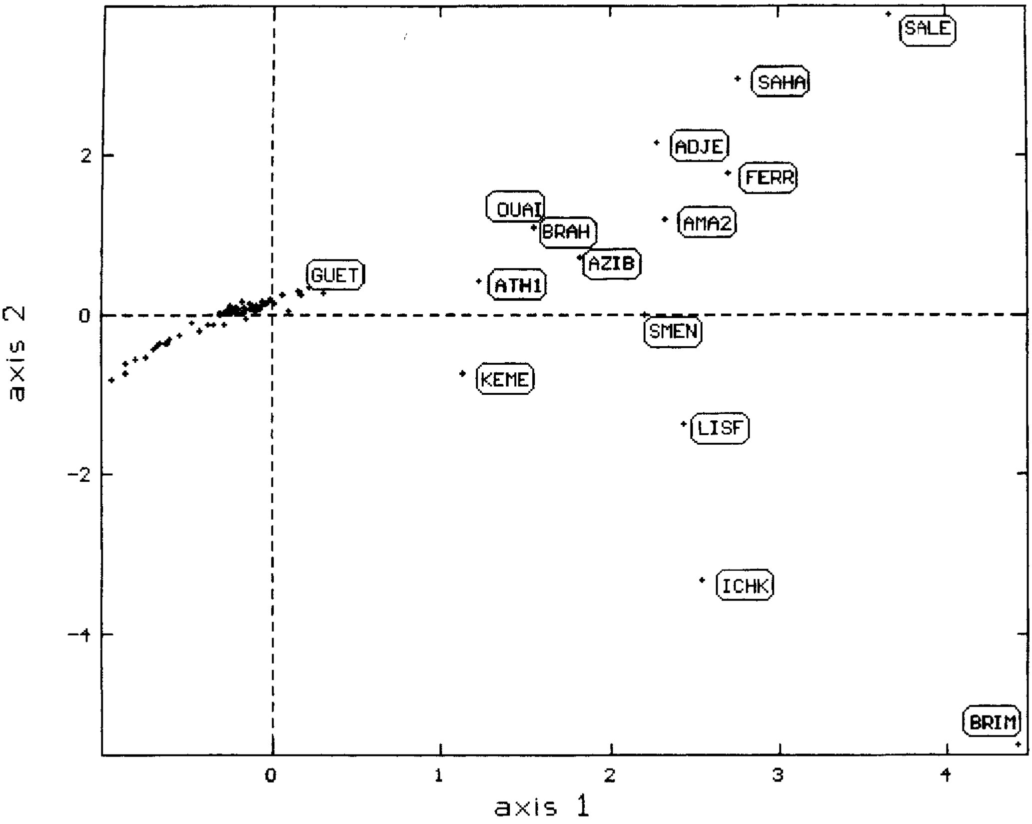

Fig. 2. Plane 1–2 of the analysis on Mediterranean localities. North African localities are boxed. Eigenvalues: axis 1, 0.63 (8.76%); axis 2, 0.50 (6.47%).

localities. Of course, one should keep in mind that one locality can be closer to another locality belonging to a different cluster than to the farthest locality of its own cluster, because all localities form a continuum.

The first dichotomy separates North African localities, except Aïn Guettara and Argoub Kemellal, from all others. We can therefore confidently conclude that, within the Mediterranean basin, there exists a North African province during Miocene–Pliocene times (corresponding chiefly to zones MN 13–14). It is characterised by taxa such as *Protatera*, *Irhoudia*, *Paraethomys miocaenicus*, *Mus*, *Golunda*, *Zramys*. Exchanges near the Miocene–Pliocene boundary are of limited impact and it is incorrect to speak of a "province paléogéographique regroupant le Maghreb et l'Europe sud-occidentale" (Benammi et al., 1995) or of a "domaine occidento-méditerranéen" (Coiffait-Martin, 1991, p. 292) because recognition of this 'province' fails to take into account the latitudinal similarities, which are greater.

Sub-provinces appear when the number of classes increases. The next splitting separates Spain, some French sites and Brisighella in Italy from those of the Eastern Mediterranean, plus the remaining French ones. The border runs therefore through France (Fig. 4). This is not unexpected, since this 'Ibero-Occitanian' province has already been recognised by Hartenberger et al. (1967), but the fit between palaeogeography (see e.g. Dercourt, 1985) and the sorting of French localities in two groups is far from perfect (the site of La Tour, East of the Rhone valley, is associated with the Spanish localities). The western Mediterranean is characterised by *Stephanomys*, *Ruscinomys*,

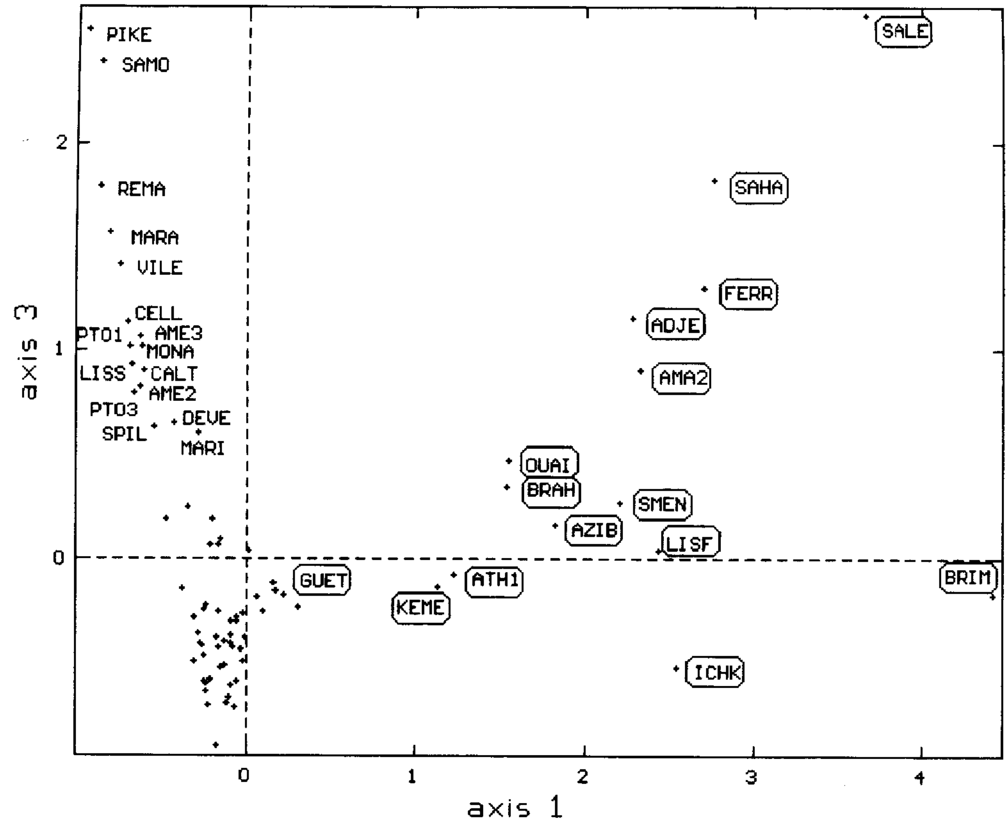

Fig. 3. Plane 2–3 of the analysis on Mediterranean localities. North African localities are boxed. Eigenvalue of axis 3: 0.48 (6.25%).

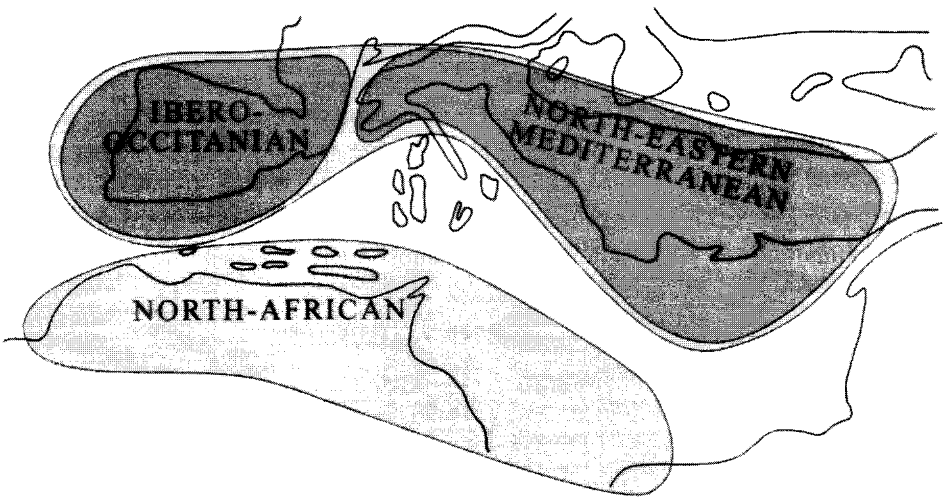

Fig. 4. The main Rodent biogeographic provinces in the Late Miocene (paleogeographic map of the Tortonian, ca. 10 Ma, from Dercourt, 1985)

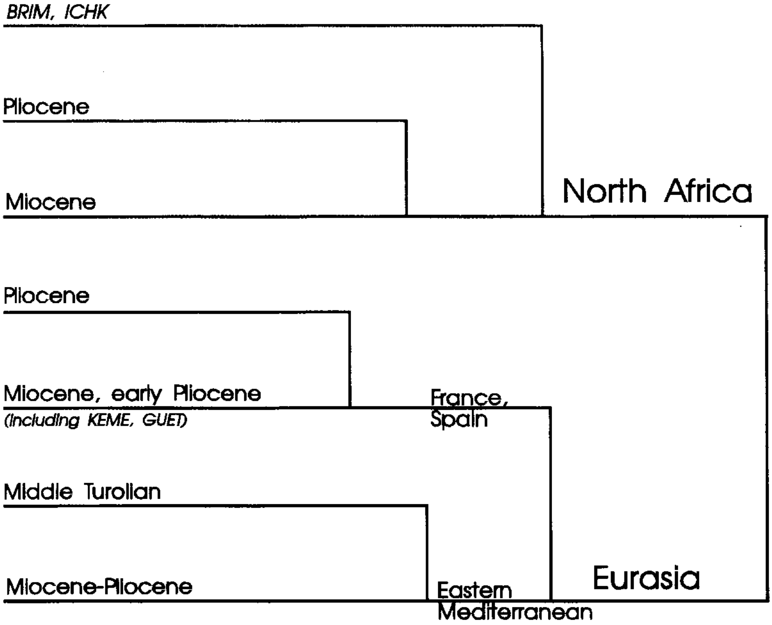

Fig. 5. A simplified hierarchical tree constructed from the results of the factor analysis on Mediterranean localities.

Cricetus kormosi and *Castillomys crusafonti*, while the eastern part has especially *Micromys*, spalacids, *Pseudomeriones*, *Keramidomys*, *Rhagapodemus* and *Occitanomys*. With four classes Aïn Brimba and Lake Ichkeul, which have *Mus* and *Paraethomys debruijni*, are separated from the remaining North African localities. These are the only Tunisian sites, but they are also among the youngest in North Africa. Further splitting isolates the oldest of the Eastern Mediterranean (Rema Marmara, Samos and Pikermi), with *Byzantinia*. With six classes, North Africa is further sub-divided on an age basis; with seven classes, Can Vilella, a Pyrenean site, is isolated. It is only with eight classes that a major break occurs within the Spanish localities, the most recent ones being separated from the earlier ones, and it is only with further splitting (12 or more classes) that more groups appear within Spain, but the factor is again chronological. Fig. 5 is a simplified version of the hierarchical tree.

5. Parsimony analysis of endemicity

This method (Rosen and Smith, 1988; Rosen, 1988; Morrone and Crisci, 1995) can be used as an alternative to factor analysis. The presence/absence matrix of locality × taxon is processed as a derived/primitive matrix of taxon × character, for input in a program of parsimonious phylogenetic analysis. Presence of a taxon in a given locality is therefore equivalent to a derived character state in a given taxon, and is used to construct monophyletic groups consisting of localities sharing one or more taxa. However, in spite of its elegance, this method has some inherent problems. First, the cladogram has to be rooted in an 'ancestor' (i.e. an ancestral association) with all taxa absent, assumed to be the primitive state. This is certainly not available, although it is certainly a better hypothesis than assuming that all taxa are present in the ancestral fauna, apomorphic state being then disappearance (Rosen and Smith, 1988). Next, if the cladogram at any given time period intends to be an area cladogram, then convergence is impossible (a taxon cannot appear separately in two areas not biogeographically linked). This must be incorporated in the computation of the cladogram (the ACCTRAN Paup option, which favours reversions rather than convergence). However, since it is impossible to distinguish between primitive absence or real reversions (extinctions) and absence due to other causes (ecological, taphonomical, incomplete sampling), absence can only be coded '0' instead of either '0' or '?', as it should be.

Despite all these drawbacks, the method has a sound theoretical basis and I have applied it to the 89 localities, divided into two groups according to their most likely age estimates: Messinian (45 localities) and post-Messinian (44 localities). When individual localities are used (that is, when there is strictly no a priori paleogeographic assumption), the consensus trees contain but a few monophyletic groups likely to have a real biogeographic significance. One of them is the non-Mediterranean Pliocene area, while North Africa appears, for both periods, 'almost monophyletic' (with the notable exceptions of Argoub Kemellal and Aïn Guettara). The overall pattern of these trees do not differ much from the dendrogram of the cluster analysis. The small number of taxa present in each locality does not allow firm groupings to be defined, some of the groups appear to have resulted by chance. This noise can be minimised by uniting localities on an a priori geographic basis, in areas (OGUs) which should, ideally, have been sampled equally intensively, because poor sampling would result in an artificially low position on the tree (Rosen, 1988)

The chosen areas (OGUs) are:

(1) North Africa;
(2) East and South Africa (for the post-Messinian only, because there are no data for earlier periods);
(3) eastern Mediterranean (Greece and Turkey);
(4) the rest of Asia;
(5) France and Italy;
(6) eastern Iberia (Levant);
(7) central Iberia (Calatayud–Teruel) and Portugal.

The consensus trees for both periods (Fig. 6) include the following monophyletic groups:

(1) France plus both parts of the Iberian peninsula;
(2) Northern Mediterranean [=group (1)+ eastern Mediterranean]

Eastern Iberia may be united with the rest of Iberia (Miocene and some of the shortest Pliocene trees) or with France (the remaining Pliocene trees), but France is never grouped with central Iberia. The main difference between both periods is that the sister group of (2) is Asia in the Messinian Miocene, but it is replaced by North Africa in the post Messinian, the rest of Africa and of Asia being then the other branch of an unsolved trichotomy on the consensus tree. After the Messinian, the northern Mediterranean province becomes more closely linked to North Africa than to the rest of Asia.

Comparison of the trees and of the apomorphies at each node also allows one to draw some tentative conclusions about migration routes and their directions:

(1) Almost all the numerous exchanges between Iberia and Eastern Mediterranean left evidence in France (the only exceptions being *Spermophilinus* and *Pseudomeriones*).
(2) Eastern Spain was a mandatory passageway for taxa entering North Africa from Western Europe, either from France or from central Iberia. This is in agreement with Agustí (1990) who noted the strong similarities of the Spanish Levant with France and central Spain in the late Turolian. Latitudinal exchanges are likely to have occurred East of Alboran rather than through Gibraltar.
(3) Southern E–W migrations are rare. Very few taxa are common to North Africa and the eastern part of Asia without also being known in France, Greece or Turkey. Thus, most of the southern Mediterranean westward migrations from Asia postulated by some authors can be refuted. Among the involved taxa, *Protatera*, cited by Agustí (1989), has since been shown by De Bruijn and Whybrow (1994) to have been incorrectly identified in Afghanistan. This leaves only *Dendromus* and *Myocricetodon*, but both genera are probably of African, rather than Asian, origin (Tong and Jaeger, 1993) and there is very little support for the 'Afro-Asiatic bioprovince' of Agustí (1990, p. 401).
(4) No taxon is common to the eastern Mediterranean and North Africa only, and there is probably no direct trans-mediterranean passage, as most authors generally agree

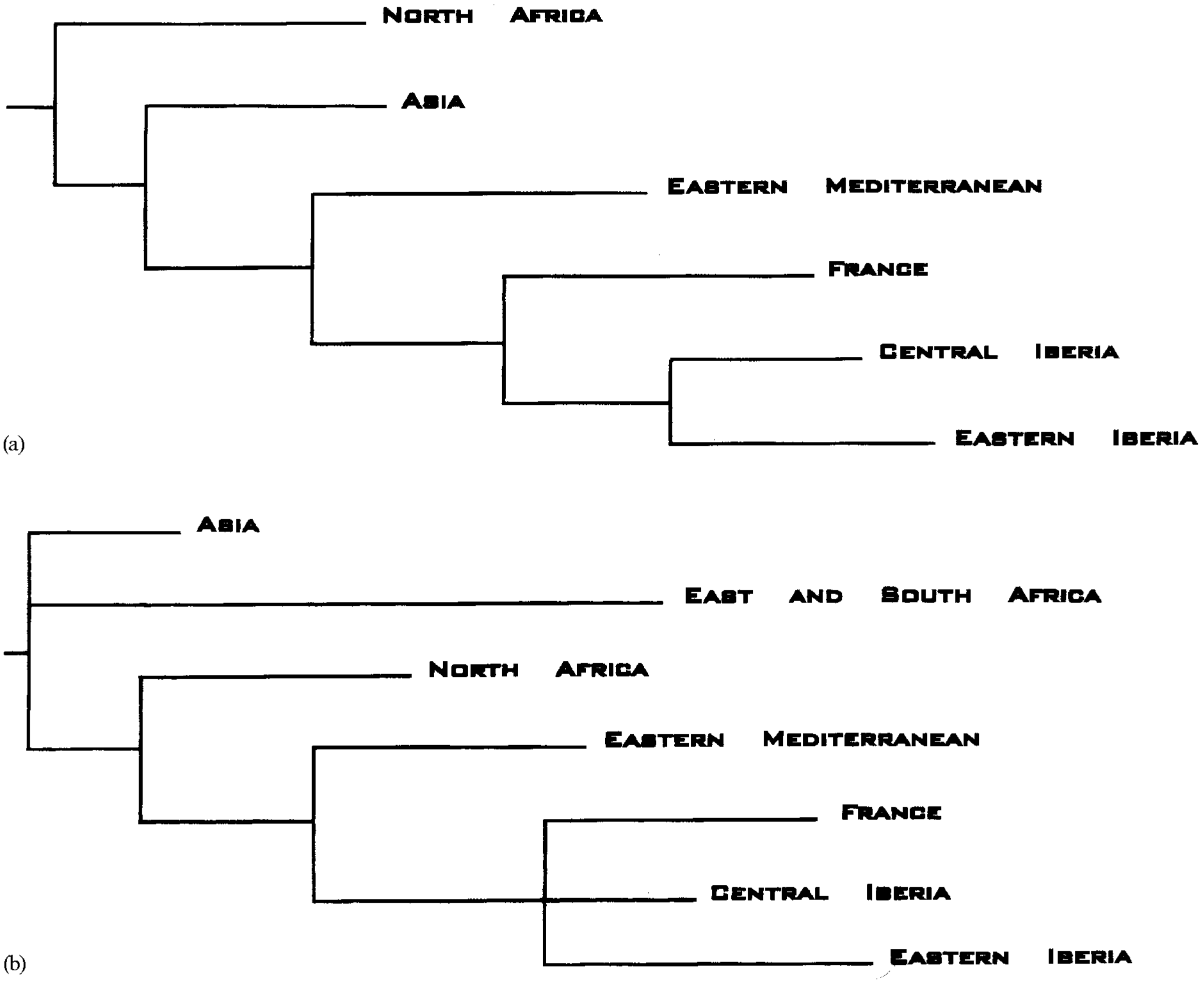

Fig. 6. The consensus tree of (A) the pre-Messinian and Messinian (roughly, MN12 and most of MN13), and (B) the post-Messinian (latest MN13 and later) OGUs. Length of the branches is proportional to the number of apomorphies, excluding reversions.

upon today. We may therefore surmise that the few alleged evidence of such a passage (e.g. *Castillomys* similar to *C.debruijni*—Coiffait-Martin, 1991) are in fact artefacts due to lack of documentation in other regions; in any case, these migrations are so few that they are of little biogeographic significance.

6. Conclusions

I believe that both methods used above, which are complementary, are much more reliable than the use of selected taxa, even if carefully studied, because they are much less sensitive to inadequate sampling, imperfect temporal placement of some localities, and even some incorrect taxonomic identifications. This is not to say that the biogeographic relationships or the Miocene–Pliocene rodent faunas of North Africa are quite clear. There is still much to learn from the Upper Miocene of the rest of Africa, but the general pattern of mostly northern circum-Mediterranean (rather than trans-Mediterranean) exchanges is unlikely to be seriously modified by future discoveries. On the whole, the Miocene–Pliocene is more a period of gradual overlapping of biogeographic realms than of sudden breaks of barriers and establishment of new corridors.

Acknowledgements

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Appendix A

Presence/absence table of the Rodent taxa, with the main references. Many of the proposed mammalian zones are approximate, especially those of the non-Mediterranean localities (see, among others, Hugueney and Mein, 1965, 1966; Adrover, 1969; Mein and Michaux, 1970; Jaeger, 1971, 1977; De Bruijn, 1974, 1976, 1989; De Bruijn et al., 1970, 1975; Van De Weerd, 1976, 1979; Montenat and De Bruijn, 1976; Sen, 1977, 1983; Jacobs, 1978; Brandy, 1979; Black et al., 1980; Agustí et al., 1981, 1989; Sabatier, 1982; Aguilar et al., 1982, 1984, 1986, 1991; Mein et al., 1983; Aguilar and Michaux, 1984; Ruiz Bustos et al., 1984; Agustí and Galobart, 1986; Ameur-Chehbeur, 1988; Agustí, 1986; Aguilar and Thaler, 1987; Pocock, 1987; Munthe, 1987; De Giuli, 1989; Sen et al., 1989; Tong, 1989; Sesé, 1989, 1991; Antunes and Mein, 1989, 1995; Alcalá and Montoya, 1990; Castillo et al., 1990; Perez and Soria, 1990; Fahlbusch, 1992; Adrover et al., 1993; Benammi, 1993; Flynn et al., 1995).

LOCALITY	ABBREVIATION	AREA	MAMMALIAN ZONE (L = Lower, U = Upper)	REFERENCES	*Apodemus*	*A.dominans*	*A.gorafensis*	*A.gudrunae*	*A.jeanteti*	*Abudhabia*	*Acomys*	*Aethomys*	*Arvicanthis*	*Atlantoxerus*	*Bathyergus*	*Blancomys*	*Byzantinia*	*Cricetus*	*C.barrierei*	*C.kormosi*	*Calomyscus*	*Castillomys*	*C.crusafonti*	*C.debruijni*	*Castoridae*	*Cryptomys*	*Cryptopterus*	*Dasymys*	*Dendromus*	*Dipoides*
AÏN BRIMBA	BRIM	A-N	MN 14U	Tong, 1989; Coiffait, 1991																										
AÏN GUETTARA	GUET	A-N	MN 13U	Brandy, 1979; Brandy & Jaeger, 1980	1				1									1	1											
AMAMA2	AMA2	A-N	MN 12S	Jaeger, 1977; Ameur, 1988; Coiffait, 1991										1																
ARG.KEMELLAL 1	KEME	A-N	MN 13	Coiffait, 1991	1			1														1								
ATHMENIA 1	ATH1	A-N	MN 15	Coiffait, 1991										1																
AZIB	AZIB	A-N	MN 14L	Benammi, 1993																										
BENI BRAHIM	BRAH	A-N	MN 12S	Coiffait, 1991																										
BOU ADJEB	ADJE	A-N	MN 12S	Coiffait, 1991																										
GUERGOUR FERROUDJ	FERR	A-N	MN 12S	Coiffait, 1991										1																
ICHKEUL	ICHK	A-N	MN 14	Jaeger, 1971; Coiffait, 1991																										
KH.EL OUAICH	OUAI	A-N	MN 12S	Jaeger, 1977; Coiffait, 1991																										
LISSASFA	LSFA	A-N	MN 14L	unpublished										1																
OUED SMENDOU	SMEN	A-N	MN 15	Coiffait, 1991										1																
SAHABI	SAHA	A-N	MN 13L	Munthe, 1987; Coiffait, 1991										1																
SIDI SALEM	SALE	A-N	MN 11	Jaeger, 1977; Ameur, 1988; Coiffait, 1991																										
HADAR SH1-3	HADA	A-E	MN 15	Sabatier, 1982+E29																										
LAETOLI BEDS	LAET	A-E	MN 15	Denys, 1990																									1	
OMO B	OMOB	A-E	MN 15	Denys, 1990									1																	
LANGEBAANWEG QSM	LGBQ	A-S	MN 14	Denys, 1990							1	1			1											1			1	
MAKAPANSGAT	MAKA	A-S	MN 15	Pocock, 1987							1	1														1		1	1	
CASTELNOU 3	CAST	E-F	MN 13U	Aguilar & al., 1991	1	1		1	1									1	1			1		1						
CELLENEUVE	CELL	E-F	MN 14L	Mein & Michaux, 1970; Aguilar & Michaux, 1984	1			1										1	1						1		1			
FONT ESTRAMAR	ESTR	E-F	MN 14	Aguilar & al., 1991	1			1	1									1	1		1									
HAUTIMAGNE	HAUT	E-F	MN 14	Mein & Michaux, 1970; Aguilar & Michaux, 1984	1													1	1								1			
LA TOUR	TOUR	E-F	MN 13U	Aguilar & al., 1982; Aguilar & Michaux, 1984	1	1										1		1		1										
LISSIEU	LISS	E-F	MN 13L	Hugueney & Mein, 1965																										
MONT HELENE	HELE	E-F	MN 15L	Aguilar & Michaux, 1984; Aguilar & al., 1986	1	1			1							1		1				1	1							
SERRAT D'EN VACQUER	SERR	E-F	MN 15L	Hugueney & Mein, 1966	1		1											1							1					
SETE	SETE	E-F	MN 15	Aguilar & Michaux, 1984; Montenat & De Bruijn, 1976a														1												
BRISIGHELLA	BRIS	E-I	MN 13U	De Giuli, 1989	1			1						1				1	1											
ESBARRONDADOIRO	ESBA	E-P	MN 13U	Antunes & Mein, 1989; 1995	1			1								1		1	1											
ALCOY	ALCO	E-S	MN 13U	Adrover, 1969; Brandy, 1979; Aguilar & Michaux, 1984	1	1												1		1										
ARQ.1/LA FONTANA	ARQ1	E-S	MN 13L	Brandy, 1979; Adrover & al., 1993	1			1								1		1		1										1
ARQUILLO 4	ARQ4	E-S	MN 13	Adrover & al., 1993												1														
BACOCHAS 1	BAC1	E-S	MN 13U	Sesé, 1989, 1991	1	1								1				1		1										
BARRANCO CANUELAS	BARR	E-S	MN 15L	Sesé, 1989, 1991	1			1														1	1							
BOTARDO C	BOTC	E-S	MN 14	Agusti, 1986; Agusti & al., 1989	1		1	1										1	1			1	1							
CAN VILELLA	VILE	E-S	MN 13U	Agusti, 1989, 1990	1			1																						
CARAVACA1	CARA	E-S	MN 13U	De Bruijn, 1974; De Bruijn & al., 1975	1				1									1	1			1	1							
CASA DEL ACERO	ACER	E-S	MN 12L	Agusti & al., 1981; Alcala & Montoya, 1990										1																
CASABLANCA M	CASM	E-S	MN 13U	Agusti & Galobart, 1986; Agusti, 1990	1			1								1		1		1	1	1	1							
CELADAS 1	CEL1	E-S	MN 13L	Mein & al., 1983; Adrover & al., 1993	1		1																							
CELADAS 2	CEL2	E-S	MN 13L	Mein & al., 1983; Adrover & al., 1993	1		1									1		1		1										
CELADAS 9	CEL9	E-S	MN 14	Mein & al., 1983; Adrover & al., 1993	1	1	1																							
CORTIJO DEL MURO	CORT	E-S	MN 15L	Sesé, 1989, 1991																		1	1							
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ESCORIHUELA	ESA	E-S	MN 16	Van de Weerd, 1976; Mein & al., 1983	1	1																1	1							
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GORAFE 4	GOR4	E-S	MN 14	Agusti, 1986; Agusti & al., 1989	1		1											1	1			1	1							
GORAFE A	GORA	E-S	MN 14	Ruiz-Bustos & al., 1984; Sesé, 1989, 1991	1		1											1	1											
HUESCAR 3	HUE3	E-S	MN 15U	Sesé, 1989, 1991												1		1	1			1	1							
LA ALBERCA	ALBE	E-S	MN 13U	De Bruijn & al., 1975														1		1		1	1							
LA CALERA	CALE	E-S	MN 14	Perez & Soria, 1990	1	1								1		1						1	1							
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LA JULIANA	JULI	E-S	MN 15L	Montenat & de Bruijn, 1976														1	1											
LIBRILLA	LIBR	E-S	MN 13L	De Bruijn & al., 1975; Brandy, 1979	1			1										1		1										
LOS MANSUETOS	MANS	E-S	MN 12U	van De Weerd, 1976; Alcala & Montoya, 1990										1																1
MASADA D.VALLE 6	MDV6	E-S	MN 13L	Van de Weerd, 1976; Adrover & al., 1993																										
MASADA D.VALLE 7	MDV7	E-S	MN 13L	Van de Weerd, 1976; Adrover & al., 1993	1			1										1		1										1
MOLINA SEGURA 9	MOL9	E-S	MN 13	Agusti & al, 1989; Agusti, 1990	1			1										1		1										
ORRIOS	ORRI	E-S	MN 14	Van de Weerd, 1976; Mein & al., 1983	1	1								1								1	1							
PINO MOJON	MOJO	E-S	MN 13U	Sesé, 1989, 1991	1			1																						
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Eliomys	*E.intermedius*	*E.truci*	*Eozapus*	*Epimeriones*	*Eutamias*	Gerb.sp.2	Gerbillidae indet	*Glirulus*	*Glis*	*Golunda*	*Graphiurus*	*Heterocephalus*	*Heteroxerus*	*Hispanomys*	*Hylopetes*	Hystricidae	*Irhoudia*	*Jaculus*	*Kanisamys*	*Karnimata*	*Keramidomys*	*Kowalskia*	*Lemniscomys*	Lophiomyidae	*Malacothrix*	*Mastomys*	*Mesocricetus*	*Micromys*	*Microtoscoptes*	*Millardia*	*Mimomys*	*Mus*	*Muscardinus*	*Myocricetodon*	*Myomimus*	*Mystromys*	*Nannocricetus*	*Occitanomys*	*O.adroveri*	*O.alcalai*	*O.brailloni*	*O.montheleni*	*O.neutrum*	*O.provocator*	*Oenomys*	*Orientalomys*	*Otomys*	*Paraethomys*	*P.abaigari*	*P.anomalus*	*P.debruijni*	*P.jaegeri*	*P.lissasfensis*
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P.meini	P.miocaenicus	Parapelomys	Parapodemus	Paraxerus	Pelinomys	Petromyscus	Pliopetaurista	Praomys	Progonomys	Promimomys	Prodontomys	Protatera	Protospermophilus	Pseudomeriones	Ruscinomys	R.europeus	R.lasallei	R.schaubi	Rhabdomys	Rhagapodemus	Rhizomyides	Stephanomys	S.donnezani	S.dubari	S.medius	S.minor	S.remblensis	S.thaleri	Saccostomus	Saidomys	Sayimys	Sciurus	Sinocricetus	Sinotamias	Sminthozapus	Spalacidae	Spermophilinus	Spermophilus	Steatomys	Stenodontomys	Tachyoryctes	Tamias	Tatera	Taterillus	Thallomys	Thryonomyidae	Trilophomys	Valerimys	Xerus	Zramys
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