

Parallel evolution in molar outline of murine rodents: the case of the extinct *Malpaisomys insularis* (Eastern Canary Islands)

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The lava mouse *Malpaisomys* was part of Pleistocene and Holocene faunas of the eastern Canary Islands; it became extinct during historical times. In order to evaluate the evolutionary processes of this endemic species, we set out to identify its relationships with possible mainland relatives. Its dental morphology was compared to a set of fossil and modern murine rodents from various phylogenetic groups, characterized by different diets and dental patterns, using a quantitative method based on a Fourier analysis of the outline of the first upper and lower molars. This morphometric analysis identified different evolutionary grades that are independent of the phylogenetic group. The first cluster is associated with primitive, asymmetric dental outlines, the second with intermediate forms linked to a more herbivorous diet. Highly differentiated forms diverge not only from the second cluster but also from each other. Our investigations reveal *Malpaisomys* to have had an intermediate dental pattern, a result which confirms previous palaeoecological interpretations of this taxon. However, conclusions about its closest mainland relative remain tentative. Based on a comparison of dental size and shape, as well as geographical considerations, a possible mainland ancestor could be either *Paraethomys* (North-African Pliocene) or *Occitanomys* (South-western European Pliocene). Such results support the hypothesis of a Pliocene colonization event, in which case *Malpaisomys* would display a normal evolutionary rate in dental size and shape, in spite of the insular context. In contrast, a late colonization by a modern representative of the African fauna would imply exceptionally high evolutionary rates compared to the background morphological evolution and a decrease in size that is unlikely under insular conditions. © 2004 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2004, 142, 555–572.

ADDITIONAL KEYWORDS: Fourier analysis – evolutionary trends – island biogeography – morphometrics – Murinae – Rodentia.

INTRODUCTION

Two alternative hypotheses have been suggested to drive the evolution of endemic insular species. These hypotheses favour either chance effects generating divergence between mainland and island lineages, or directional evolutionary trends within each island (Whittaker, 1998). Chance effects are related to the process of colonization. The more remote the island, the most likely it is to be colonized by a population of only a few individuals. The founder effect (Mayr, 1954) corresponds to a bias in the genetic variability between the mainland source population and the indi-

viduals founding a new colony. This effect may be subsequently enhanced by genetic drift. Alternatively, directional evolutionary trends have been recognized on islands, especially regarding size. Compared to their mainland relatives, small mammals tend to become larger (Lomolino, 1985): as many as 85% of island rodents could be characterized by this insular gigantism (Foster, 1964). Selective forces typical of insular environments have also been argued to cause parallel skeletal changes in island rodents (Pergams & Ashley, 2001). Selective forces might also be similar to those on the mainland (e.g. related to climatic regime), but the absence of gene flow between island and mainland populations might favour local adaptations compared to those on the mainland (Renaud & Millien, 2001). All the above arguments see islands as peculiar

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evolutionary environments in which divergences between island and mainland stock occur. However, it has also been suggested that island endemics represent relicts of extinct mainland populations (Cronk, 1992). Evolution on islands therefore provides an opportunity to investigate the complex relationship between chance effects, response to selection, and constraints to evolution such as phylogenetic inheritance.

The lava mouse *Malpaisomys insularis* is an extinct endemic rodent from the eastern Canary Islands. It exhibits peculiar morphological characteristics differentiating it from mainland taxa (Hutterer, López-Martínez & Michaux, 1988; Boye *et al.*, 1992). It thus provides a valuable case-study to investigate the evolutionary processes that led to its differentiation. The extinction of the taxon means that comparisons with its closest mainland relatives have to be based on morphological characters. Molar morphology is influenced by both phylogeny and ecology in rodents (Misonne, 1969) and is the only information available for fossil lineages. Hence, in our study, the size and shape of the first upper and lower molars were quantified on modern and fossil murine rodents including *Malpaisomys*. Molar shape was approximated by its outline and analysed using Fourier transform. The pattern of size and shape differentiation was investigated in order to assess the relative influence of phylogeny and ecology. In order to compare this large-scale signal to small-scale patterns of insular evolution, different populations of *Malpaisomys* which varied in age and location (main island or nearby islet) were also compared. These analyses allowed us to assess evolutionary patterns among mainland taxa and among *Malpaisomys* populations, and to evaluate the evolutionary significance of different hypotheses of colonization by a mainland ancestor.

BACKGROUND ON *MALPAISOMYS* AND ITS MAINLAND RELATIVES

Malpaisomys insularis is known from Holocene and Pleistocene deposits (Hutterer *et al.*, 1988; Michaux, Hutterer & López-Martínez, 1991; Castillo, Martín-González & Coello, 2001) in the eastern Canary Islands, including Fuerteventura, Lanzarote and nearby islets (Fig. 1). It became extinct during historical times, probably because of the arrival of man (Boye *et al.*, 1992). *Malpaisomys* owes its name to the Spanish word, *malpaís*, meaning lava fields where its fossil remains are sometimes found in cavities. A study of its skeletal characteristics suggested that *Malpaisomys* lived in fissures opened in the lava fields (Boye *et al.*, 1992).

Its phylogeny, based on dental or skeletal characters, can at present only be hypothesized; these characters can be of poor value for phylogenetic

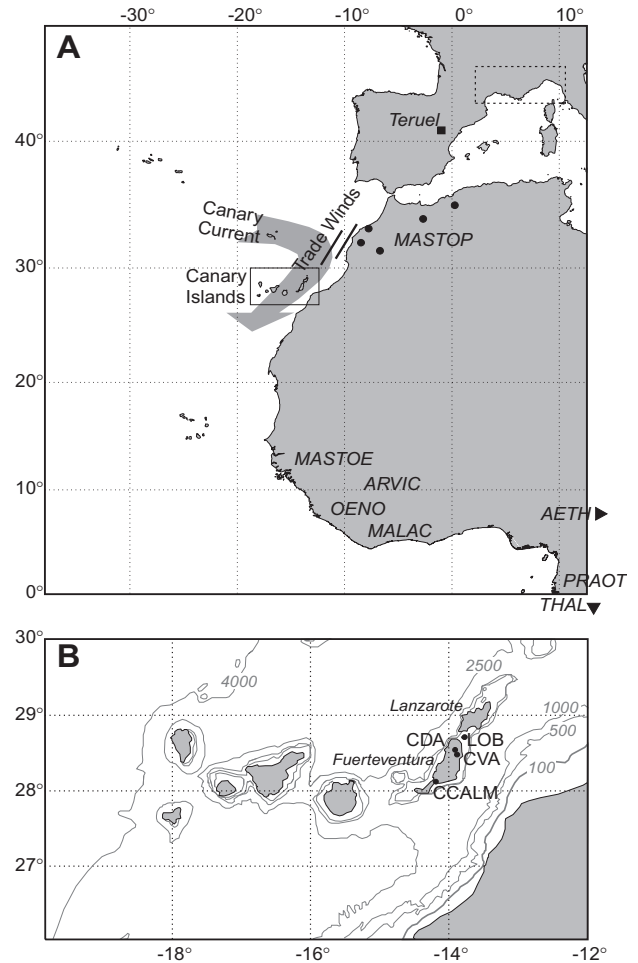


Figure 1. Geographical context and location of the samples examined in the present study. A, schematic locations of modern and fossil samples used for comparison with *Malpaisomys*. Modern taxa include *Oenomys ornatus* (OENO), *Mastomys peregrinus* (MASTOP) and *M. erythroleucus* (MASTOE), *Arvicanthis* sp. (ARVIC), *Malacomys* sp. (MALAC), *Aethomys hindei* (AETH), *Thalomys* sp. (THAL) and *Praomys tullbergi* (PRAOT). The south-west European lineage leading from *Progonomys hispanicus* to *Occitanomys* and *Stephanomys* was sampled in the Teruel Basin and in Southern France (box with dotted outline). North African localities of *Paraethomys* are shown by black dots. Main oceanographic and atmospheric circulation patterns around Canary Islands are indicated. B, location of the *Malpaisomys* deposits. Bathymetric data are shown (source GEBCO). The thick grey line close to the coast of the mainland (100 m below current sea level) may correspond to the shoreline during the glacial periods.

reconstruction, especially because of cases of convergent evolution. *Malpaisomys* was first interpreted as related to Acomyinae (Hutterer *et al.*, 1988). Acomyinae now constitutes a genetically well-identified group

showing morphological convergence in dental pattern with the Murinae, in particular in the first two upper cheek teeth (Chevret, Michaux & Catzeflis, 1993). Immunogenetic comparisons, however, cast some doubt on the relationships of *Malpaisomys* and *Acomys*, suggesting that *Malpaisomys* was more closely related to Murinae than to Acomyinae (Montgelard, 1992). This interpretation has been reinforced by the reconsideration of some dental features typical of murine rodents, such as the structure of the third upper molar (Denys & Michaux, 1992). Consequently, *Malpaisomys* is now considered to be a true murine. In addition, *Malpaisomys* displays a dental specialization termed stephanodonty (Schaub, 1938; Misonne, 1969), which is characterized by the swelling of the cusps and the development of longitudinal crests that extend the cusps and join them in a garland-like pattern on the upper molars. Such a trend has been interpreted as an adaptation to a diet rich in green vegetation or grass by analogy with the extant African stephanodont murines *Oenomys* (Dieterlen, 1967) and *Aethomys* (Denys, 1994), and functional morphological arguments (Michaux, 1978; van Dam, 1997). The similarity of the dental patterns is stressed by the grouping of *Malpaisomys* together with the stephanodont murines *Oenomys* and *Stephanomys* (López-Martínez, Michaux & Hutterer, 1998).

Stephanodonty in *Malpaisomys* could be the result either of evolution from a stephanodont ancestor or of convergent evolution. In order to investigate both hypotheses, we compared *Malpaisomys* with murine rodents showing a stephanodont trend and with taxa exhibiting a basic murine dental pattern (Fig. 2). Stephanodont rodents include several fossil taxa and some tropical extant species. An evolutionary lineage leading to the evolution of stephanodonty starts in south-western Europe with *Progonomys hispanicus* evolving into *Occitanomys*. A cladogenesis around 7 Mya leads to *Occitanomys alcalai* on the one hand and to *Stephanomys* on the other (Michaux, 1971; van de Weerd, 1976; van Dam, 1997). The evolution along this lineage leads from small and primitive molars in *P. hispanicus* to large and specialized, highly stephanodont molars in *Stephanomys*, with *Occitanomys* having intermediate features (van de Weerd, 1976; Cordy, 1978; van Dam, 1997). Stephanodonty evolved independently along the lineage of *Paraethomys* (Jaeger, 1977; Coiffait, 1991; Benammi *et al.*, 1995, 1996), a genus characteristic of North African rodent fauna from the Late Miocene until its extinction late in the Pleistocene (Jaeger, 1977; Jaeger, Michaux & Thaler, 1975). *Progonomys cathaloi* was present earlier than *Paraethomys* in North Africa, and compared to the latter it is characterized by a more primitive evolutionary stage in dental morphology. Consequently, it is considered in the present study as the morphological

reference for an ancestor of the *Paraethomys* lineage. Within extant species, *Oenomys* displays complete stephanodonty (Misonne, 1969) while *Aethomys* shows some stephanodont characteristics (Denys, 1994).

Malacomys, *Praomys* and *Mastomys* were chosen as examples of rodents characterized by a basic dental pattern associated with an omnivorous diet. *Mastomys peregrinus* was considered because its geographical range, including western North Africa, makes a colonization of the Canary Islands by this species more likely than by a tropical taxon (Fig. 1). The arvicanthine group (Ducroz, Volobouev & Granjon, 2001) includes murine rodents with a herbivorous diet. *Thallomys* and *Arvicanthis* are part of this group but do not display stephanodont trends, unlike *Aethomys* and *Oenomys*. However *Thallomys* and *Arvicanthis* were included in order to evaluate the role of diet on the shape of molars.

MATERIAL AND METHODS

MATERIAL

The material related to *Malpaisomys* consists of 71 first upper molars (M1/) and 80 first lower molars (M/1) from four localities in Fuerteventura and Lobos, the smaller island next to it (Fig. 1B). All deposits except Costa Calma correspond to lava tubes in the middle of ancient lava fields. Using radiocarbon dating and interpolations using the observed faunas, we were able to estimate an age for three of the localities. The fourth locality, in Lobos, is probably of Holocene age due to the presence of *Mus* in the deposit (Table 1) (Hutterer *et al.*, 1988; Michaux *et al.*, 1991, 1996; Boye *et al.*, 1992; Castillo *et al.*, 2001).

The proposed North African lineage of *Paraethomys* has been analysed, using nine deposits (58 M1/, 76 M/1) with *Progonomys cathaloi* (3 M1/, 3 M/1) as a reference for a primitive stage of the lineage. Age estimates are based on biostratigraphy, radiometric dating and magnetostratigraphy (Benammi *et al.*, 1996; Renaud *et al.*, 1999a). The evolutionary lineage from *Progonomys hispanicus* to *Occitanomys* and *Stephanomys* was considered using a set of Spanish and French deposits (238 M1/, 219 M/1). Ages were estimated by linear interpolations based on magneto-, litho- and biostratigraphy of deposits in the Teruel basin in Spain (Fig. 1A) (van Dam, 1997; van Dam *et al.*, 2001; Renaud & van Dam, 2002) and southern France (Aguilar *et al.*, 2002). The ages were calibrated according to a new model established from deposits in southern France (Aguilar *et al.*, 2004). Sixty-eight modern specimens (Museum National d'Histoire Naturelle, Paris) belonging to eight taxa are included for comparison (Table 1).

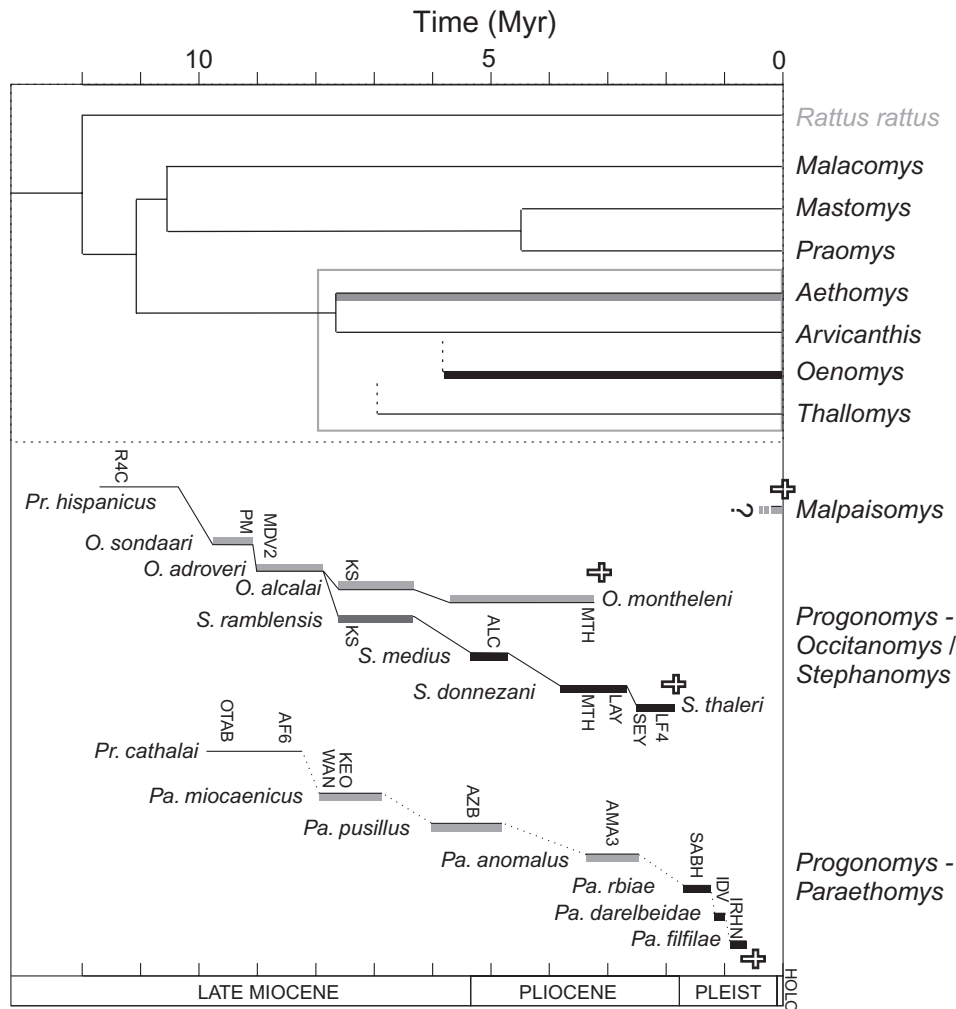


Figure 2. Schematic representation of the modern and fossil murine rodents compared to *Malpaisomys*. Top, molecular phylogeny after Chevret (1994) and Chevret *et al.* (2001). A calibration of the time of divergence between taxa is given by reference to the divergence of the *Rattus rattus* lineage, estimated as having occurred 12 Mya (Chevret *et al.*, 2001). The grey box includes the arvicanthine rodents, characterized by a herbivorous diet. Bottom, fossil lineages with investigated localities. Thick grey lines indicate taxa with stephanodont characteristics, thick black lines, complete stephanodonta. Crosses indicate extinct taxa.

FOURIER ANALYSIS OF THE MOLAR OUTLINE

A description of the murine molars based on outline analysis appears to provide a valuable description of the overall morphology of the teeth, especially the position of the main cusps, which is not affected by heavy modification due to the varying stages of wear. This method has been applied successfully to analysis of geographical and evolutionary differentiation in rodents (Renaud *et al.*, 1999a,b; Renaud, 1999; Renaud & van Dam, 2002).

The outline corresponds to a two-dimensional projection of the tooth viewed from the occlusal surface. All molars were measured as outlines of left teeth.

Hence, mirror images of right molars were considered, in order to compare their shape with that of the left molars. Then, for each tooth, the x and y coordinates of 64 points equally spaced along the outline were extracted semiautomatically using an optical image analyser (Optimas 6.5), and thereafter analysed by a radial Fourier transform (RFT). The starting point of the outline was defined as the maximum point of curvature of the anterior part of the tooth. From the x , y coordinates of the points, 64 radii corresponding to the distance of each point from the centre of gravity of the outline were calculated. A Fourier transform was then applied to this set of 64 radii. The outline is thus expressed as a finite sum of trigonometric functions of

Table 1. The murine rodent samples included *Malpaisomys* (MALP), modern groups used for comparisons (MODERN), and fossil representatives belonging to the *Paraethomys* lineage (PARAET) and to the *Occitanomys–Stephanomys* lineage (STEPH). Codes are given, country of trapping for modern samples and deposit for fossil samples, generic and specific determination, approximate age (in Myr), and number of upper (M1/) and lower (M/1) molars measured. Period: MOD, modern; HOL, Holocene; PLEI, Pleistocene; PLIO, Pliocene; MIO, Miocene

Group	Code	Site	Genus	Species	Period	Age	M1/	M/1
MALP	CDA	Cueva de Arena	<i>Malpaisomys</i>	<i>insularis</i>	HOL	600 BP	25	20
	CVA4	Cueva Villaverde A4 IV	<i>Malpaisomys</i>	<i>insularis</i>	HOL	1800 BP	30	30
	CCALM	Costa Calma	<i>Malpaisomys</i>	<i>insularis</i>	PLEI	25000 BP	2	10
	LOB4	Lobos 4	<i>Malpaisomys</i>	<i>insularis</i>	HOL	–	14	20
MODERN	AETH	RCA	<i>Aethomys</i>	<i>hindei</i>	MOD	0	5	5
	ARVIC	Ivory Coast, Senegal	<i>Arvicanthis</i>	sp.	MOD	0	2	2
	MALAC	Ivory Coast	<i>Malacomys</i>	sp.	MOD	0	10	10
	MASTOE	Senegal	<i>Mastomys</i>	<i>erythroleucus</i>	MOD	0	3	3
	MASTOP	Morocco	<i>Mastomys</i>	<i>peregrinus</i>	MOD	0	8	8
	OENO-CIV	Ivory Coast	<i>Oenomys</i>	<i>ornatus</i>	MOD	0	5	5
	OENO-GHA	Ghana	<i>Oenomys</i>	<i>ornatus</i>	MOD	0	4	4
	OENO-GUI	Guinea	<i>Oenomys</i>	<i>ornatus</i>	MOD	0	23	23
	PRAOT	Equatorial Guinea	<i>Praomys</i>	<i>tullbergi</i>	MOD	0	6	6
	THAL	Angola, Somalia	<i>Thallomys</i>	sp.	MOD	0	2	2
PARAET	IRHN	Irhoud Neanderthal	<i>Paraethomys</i>	<i>filifilae</i>	PLEI	0.6	13	27
	IDV	Irhoud DV	<i>Paraethomys</i>	<i>darelbeidae</i>	PLEI	1	30	30
	SABH	Sidi Abdallah 1	<i>Paraethomys</i>	<i>rbiae</i>	PLEI	1.5	0	7
	AMA3	Amama 3	<i>Paraethomys</i>	<i>anomalus</i>	PLIO	2.9	7	5
	AZB	Azib	<i>Paraethomys</i>	<i>pusillus</i>	PLIO	5.3	4	1
	KEO	Khendek el Ouaich	<i>Paraethomys</i>	<i>miocaenicus</i>	PLIO	7.7	2	4
	WAN	Wanou	<i>Paraethomys</i>	cf. <i>miocaenicus</i>	PLIO	7.8	2	2
	AF6	Afoud 6	<i>Progonomys</i>	<i>cathalai</i>	PLIO	8.5	0	3
	PC-OTAB	Ouet Tabia	<i>Progonomys</i>	<i>cathalai</i>	PLIO	9.5	3	0
	STEPH	S-LF4	Lo Fournas 4	<i>Stephanomys</i>	<i>thaleri</i>	PLIO	2	30
S-SEY		Seynes	<i>Stephanomys</i>	<i>thaleri</i>	PLIO	2.5	30	30
S-LAY		Layna	<i>Stephanomys</i>	<i>donnezani</i>	PLIO	2.9	30	30
O-MTH		Mont-Hélène	<i>Occitanomys</i>	<i>montheleni</i>	PLIO	3.3	30	24
S-MTH		Mont-Hélène	<i>Stephanomys</i>	<i>donnezani</i>	PLIO	3.3	30	30
S-ALC		Alcoy	<i>Stephanomys</i>	<i>medius</i>	PLIO	5	2	6
S-KS		Las Casiones	<i>Stephanomys</i>	<i>ramblensis</i>	MIO	7.3	20	15
O-KS		Las Casiones	<i>Occitanomys</i>	<i>alcalai</i>	MIO	7.3	18	15
OA-MDV2		Masada del Valle 2	<i>Occitanomys</i>	<i>adroveri</i>	MIO	9	20	15
OS-PM		Puente Minero	<i>Occitanomys</i>	<i>sondaari</i>	MIO	9.2	20	15
PH-R4C	La Roma 4C	<i>Progonomys</i>	<i>hispanicus</i>	MIO	11.3	8	9	

decreasing wavelength (harmonics), each weighted by two Fourier coefficients A_n and B_n . Any outline is therefore described by the corresponding set of Fourier coefficients. The 0th harmonic, A_0 , is proportional to the size of each specimen and is used to standardize all the Fourier coefficients, in order to retain shape information only. A reconstruction of the outline corresponding to any set of Fourier coefficients can be obtained using an inverse Fourier transform.

A characteristic of Fourier harmonics is that the higher the rank of the harmonic, the more details of the outline are described. This property can be used to filter measurement noise, which increases with

harmonic rank. A study of specimens from the *Progonomys–Occitanomys/Stephanomys* lineage indicated that the effect of the measurement error could be limited by considering only Fourier coefficients up to the ninth harmonic for the upper molars, and up to the sixth for the lower (Renaud *et al.*, 1999b). A homologous definition of the starting point can be problematic for the first lower molars because of the development in some taxa of additional cusplets. Hence, only the harmonic amplitudes (i.e. square root of the sum of the squared Fourier coefficients) were considered in the subsequent analyses for the lower molars, because they are independent of the starting

point. Unfortunately, considering only the amplitudes hinders the reconstruction of outlines by an inverse Fourier transform.

STATISTICAL ANALYSES

A set of 18 Fourier coefficients (i.e. nine harmonics) for each first upper molar and of six amplitudes (i.e. six harmonics) for each first lower molar was obtained. These coefficients were standardized in terms of size and therefore correspond to shape information only. A multivariate analysis of variance (MANOVA) was performed on these variables in order to evaluate the importance of the among-group differentiation relative to the within-group variation. In the analyses, the grouping variable corresponds to species/deposit or locality. A test of significance for among-group differences (Wilks' lambda) is included. Associated with the MANOVA, canonical functions were estimated, the first of which was sufficient to account for the most important group differences (Manly, 1994). The scores of the group means can be plotted on these canonical axes to visualize the pattern of morphological differentiation. In order to investigate whether the canonical analysis provided a valuable summary of the morphological differentiation, a clustering analysis was performed on the set of Fourier coefficients up to the ninth harmonic for the first upper molars: Euclidean distances were also calculated among group means and a UPGMA (unweighted pair-group method, arithmetic average) cluster analysis was then applied to this distance matrix and visualized as a phenetic tree.

Size, estimated by A_0 , corresponds to an univariate parameter. Its differentiation was therefore tested using an analysis of variance (ANOVA) and t -tests. Statistical analyses were performed using Systat 10 and NTsys-pc v. 2.1 (Rohlf, 1998).

ESTIMATION OF EVOLUTIONARY RATES

Size and shape evolution were estimated independently of the multivariate analyses, directly onto the Fourier coefficients. Size distances were calculated as differences along A_0 between group means. Shape distances were calculated among group means on the 18 Fourier coefficients of the first upper molar outlines. One way to calculate evolutionary rates is to plot morphological distance against time interval; rates are the slope of the linear regressions, if significant. A second way is to divide morphological distance by time interval; this can produce high values for short time-intervals, an effect which can be reduced by logarithmic transformation. Negative values hinder this transformation. Hence, the formula used is $\log(|\text{morphological distance}|/\text{time interval})$.

The whole distance matrix among groups was not taken into account because of the difficulty involved in assessing the time interval since divergence for some pairs of samples. For both fossil lineages, evolutionary rates were calculated between a given stage and all previous stages, assuming a direct ancestor–descendent relationship.

Evolutionary rates cannot be estimated in a similar way for modern taxa. Time of divergence was estimated from molecular studies proposing dating based on a molecular clock hypothesis (Chevret, 1994; Chevret *et al.*, 2001). The basal divergence between the *Praomys* group, *Malacomys* and the arvicanthine group was estimated at 11 Mya. Assuming random evolution since divergence (Schluter, 2000), the rate of morphological evolution can be estimated as half the morphological difference between both modern taxa divided by the time interval since divergence.

Several hypotheses were considered for *Malpaisomys*. Rates of divergence were estimated between it and the different fossil samples. For the modern samples, a hypothesis was formulated with colonization of the eastern Canary Islands estimated at 140 kya, when the sea level was more than 100 m below its present level due to glacial conditions. This should have decreased the distance from the mainland to the eastern Canary Islands to 70–100 km (Fig. 1B). Additionally, a rate of divergence was evaluated within *Malpaisomys* between the Pleistocene population of Costa Calma and the Holocene one of CVA4.

RESULTS

COMPARISON OF *MALPAISOMYS* AND POSSIBLE RELATIVES

Malpaisomys has been compared to different stages of the *Progonomys*–*Occitanomys*/*Stephanomys* and *Paraethomys* lineages, to *Progonomys cathalai* and to several modern taxa (Table 1). An important morphological differentiation exists for the first upper and lower molars ($P < 0.001$).

For the upper molars, the first two canonical axes display most of the among-group differentiation (Fig. 3A). In the plane defined by the first (CA1, 46.3% of the among-group variance) and the second axes (CA2, 18.2%), the first cluster includes *Progonomys* associated with *Mastomys*, *Praomys* and *Malacomys*. All of these murine teeth are characterized by an asymmetrical outline. They also share a basic omnivorous murine diet. From this 'omnivorous' cluster the second cluster diverges along both CA1 and 2, including murines with broader and more symmetrical molar outlines. Among these taxa, those with a known ecology share a trend towards a herbivorous diet. This cluster of 'intermediate' outlines includes

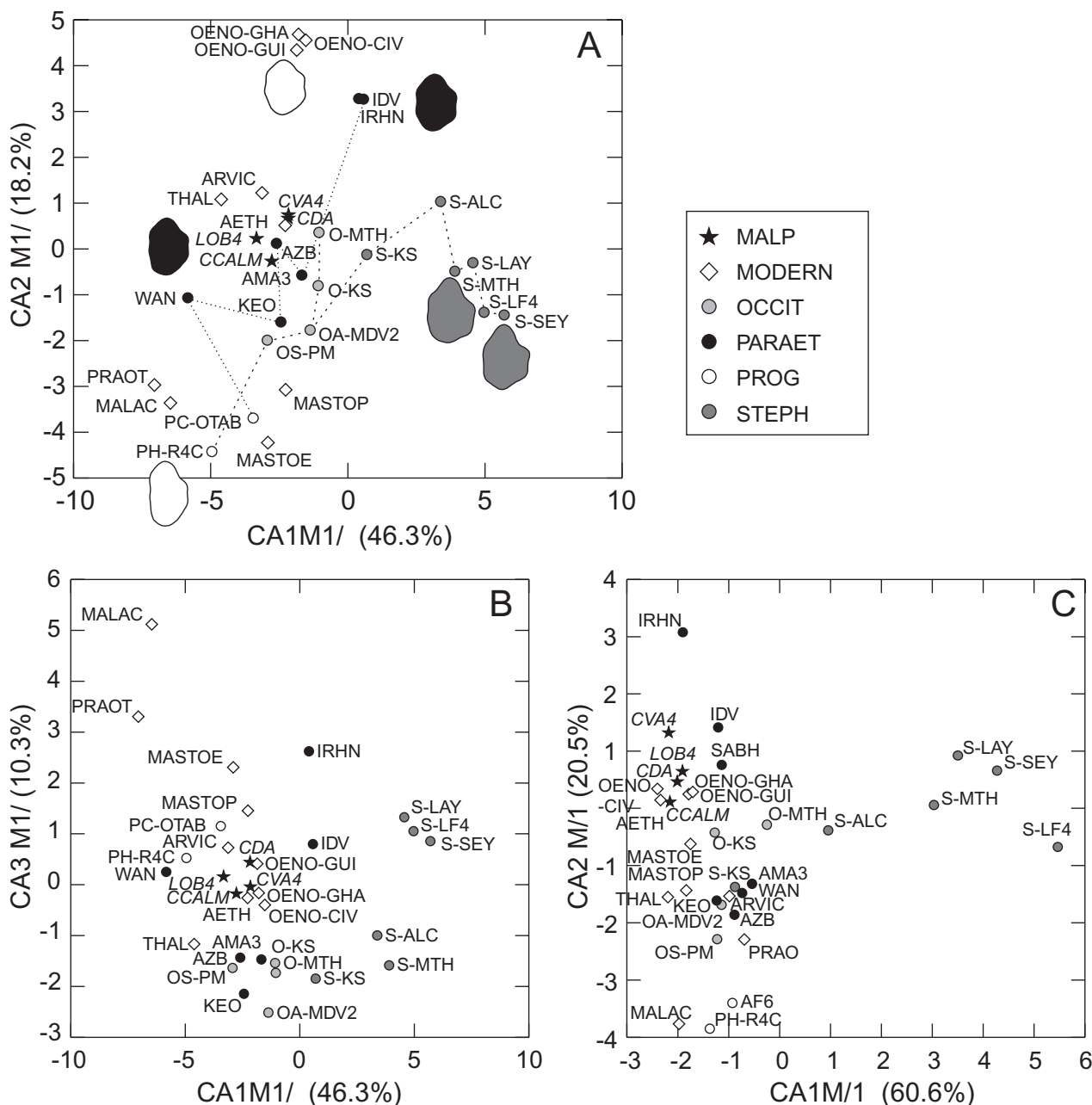


Figure 3. Morphological differentiation of the dental outline among murine rodents. A, upper molars. Group means on CA1 and 2. Dotted lines show the fossil lineages leading from *Progonomys hispanicus* to *Occitanomys* and to *Stephanomys*, and from *Pr. catalai* to *Paraethomys*. Outlines correspond to some group means. B, upper molars, CA1 and 3. C, lower molars, CA1 and 2. For locality and sample abbreviations see Table 1.

Mio-Pliocene *Paraethomys*, *Occitanomys*, the arvicanthines (except *Oenomys*), and *Malpaisomys*. From this cluster, *Stephanomys* (along CA1), the Pleistocene *Paraethomys* (mostly along CA2 with a component along CA1), and *Oenomys* (along CA2) show a further divergence. All these taxa are characterized by a typical stephanodont dental pattern associated with broader and more symmetrical outlines.

The modern taxa *Praomys*, *Malacomys* and to a lesser extent *Mastomys* (Fig. 3B) are especially isolated on the third axis (10.3% of among-group variance). It appears to correspond to a phylogenetic signal of the *Praomys*–*Malacomys* group.

The results based on the first lower molars (Fig. 3C) are less clear but suggest similar features than those based on the upper molars (Fig. 3A, B). The differen-

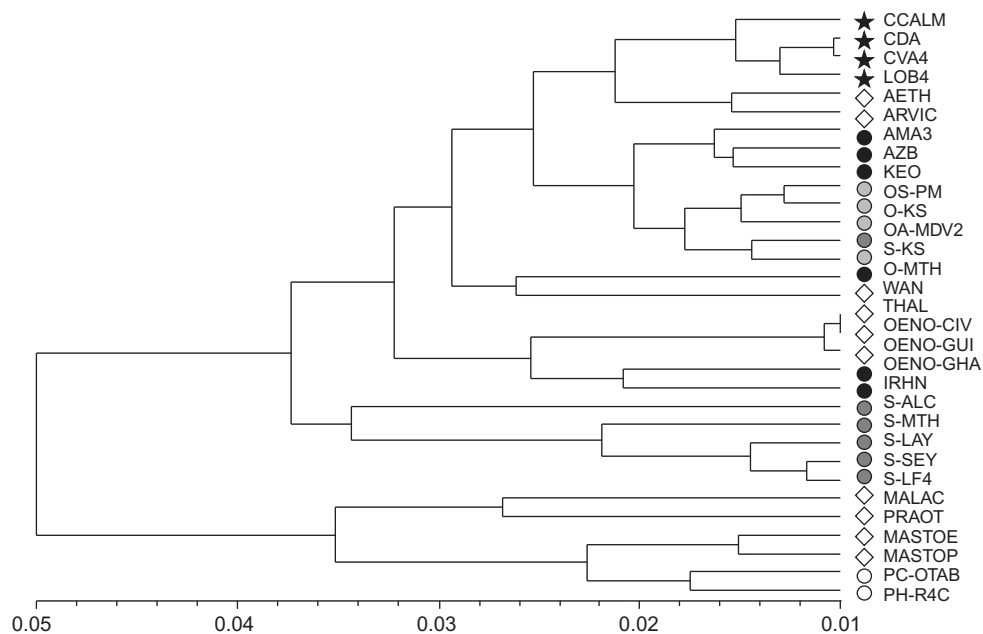


Figure 4. Cluster analysis of the shape of the upper molar. Euclidean distances between group means were calculated based on Fourier coefficients up to the ninth harmonic (CF9). Clustering method was UPGMA (unweighted pair-group method, arithmetic average). Symbols as per Fig. 3. For locality and sample abbreviations see Table 1.

tiation along CA1 (60.6% of the among-group variance) corresponds to a considerable divergence of *Stephanomys*, the most recent (LF4) being the most extreme. Along CA2 (20.5% of variance) *Progonomys*, associated with *Malacomys*, is opposed to Pleistocene *Paraethomys*. In between are found two clusters; the first includes the oldest *Occitanomys* and the Mio-Pliocene *Paraethomys*, *Mastomys*, *Arvicanthis* and *Thallomys*, the second includes more recent *Occitanomys*, *Oenomys* and *Malpaisomys*. CA2 therefore displays a trend from primitive towards more derived outlines, and *Malpaisomys* is associated with rather derived ones.

The distribution of the taxa on these canonical axes might appear to be a simplification of the morphological signal and thus undermine the interpretation of the morphological differentiation as an ecological signal showing evolutionary grades. We therefore complemented the multivariate analysis by a cluster analysis of the raw data, focusing on the first upper molar shape. Distances were calculated from the Fourier coefficients and a phenetic tree was constructed using a UPGMA algorithm (Fig. 4). In agreement with the patterns observed on the canonical axes, outlines interpreted as 'omnivorous' are grouped together, including *Progonomys*, *Malacomys*, *Praomys* and *Mastomys*. *Stephanomys* appears as highly divergent. Derived, stephanodont *Oenomys* and Pleistocene *Paraethomys* are clustered and clearly separate from a cluster of outlines characterized by an intermediate

stage of evolution: *Occitanomys*, Mio-Pliocene *Paraethomys*, the arvicanthines *Aethomys* and *Arvicanthis*, and *Malpaisomys*.

FINE-SCALE DIFFERENTIATION WITHIN *MALPAISOMYS*

Size differences are significant among the samples of *Malpaisomys*, for both the first upper ($P < 0.001$) and lower molars ($P = 0.002$). The data show that no gigantism characterizes the population from Lobos (Fig. 5A, B), which is rather smaller than the populations of Fuerteventura. The oldest (Pleistocene) population from Fuerteventura (Costa Calma) is larger than the Holocene samples.

Shape differentiation is also significant for both upper and lower molars ($P < 0.001$). Patterns are similar for the two sets of data. The most important difference characterizes the population from Lobos (Fig. 5C, D). The Costa Calma population seems slightly divergent for the lower molars, the reduced sample size of the upper molars hindering any robust analysis. Testing two-by-two differences between samples (Table 2) corroborates these results.

SIZE AND SHAPE EVOLUTION OVER TIME

As we included extinct species in our study, it seemed necessary to examine evolutionary patterns over time in order both to interpret morphological differentiation on a long time-scale and to better evaluate the

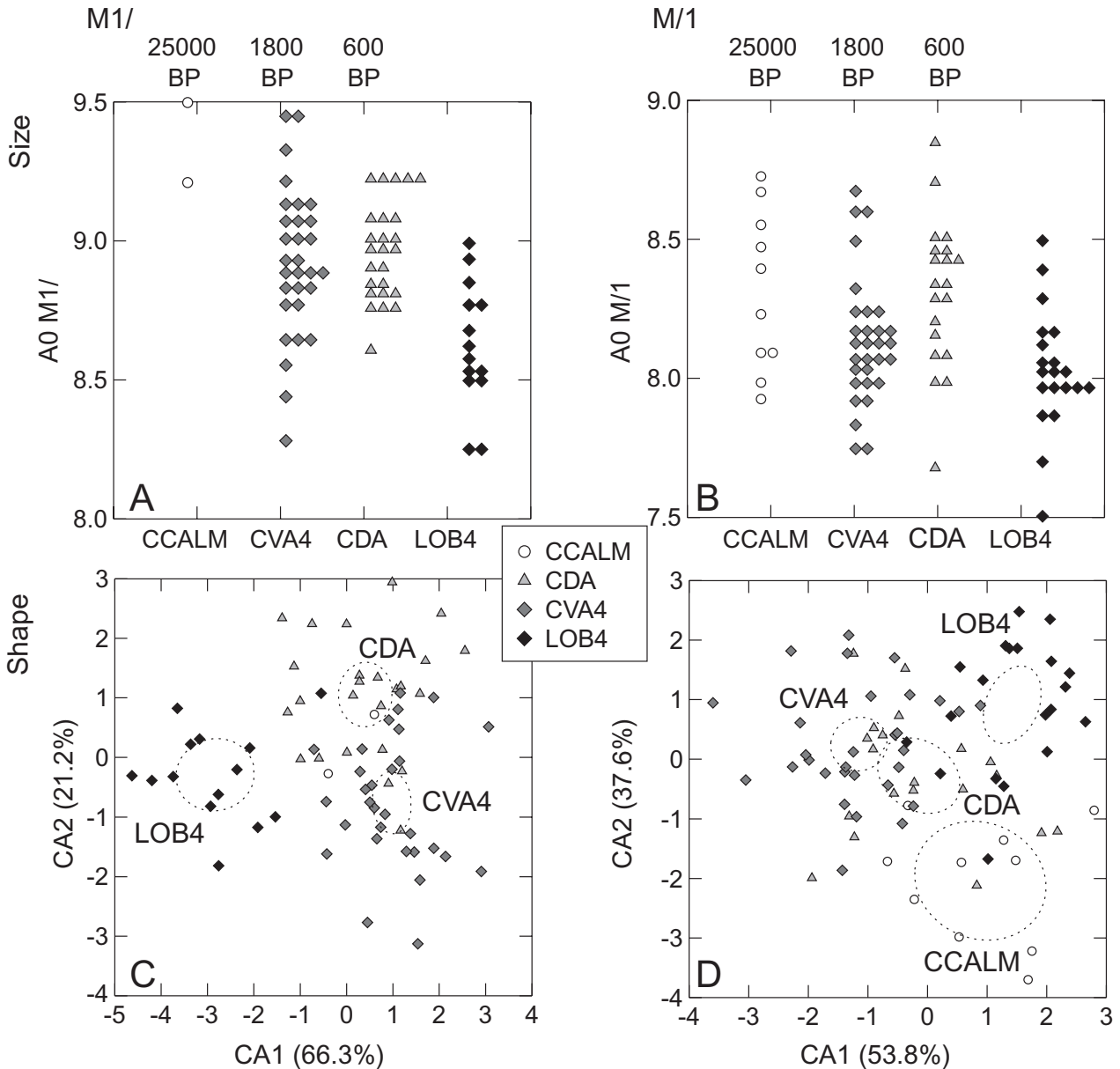


Figure 5. Morphological differentiation within *Malpaisomys*. Size of the first upper (A) and lower (B) molars. Shape of the first upper (C) and lower (D) molars, estimated by the scores on the first and second canonical axes of the analysis of *Malpaisomys*. The dotted ellipses indicate the 95% confidence interval for each sample.

processes which might have led to the insular differentiation of *Malpaisomys*.

Size and shape of the first upper molars were plotted as a function of their estimated age. The amplitude of the temporal variations was compared to the amount of morphological differentiation among modern taxa and *Malpaisomys* (Fig. 6). A trend of increasing size is displayed in both fossil lineages, with a similar pattern of large size increase in most recent samples (from MTH to LAY in the *Stephanomys* lin-

age, and from AMA3 to IDV in the *Paraethomys* lineage). Compared to these patterns, *Malpaisomys* is of intermediate size, closest to the latest samples before the step up in size. When compared to the modern taxa, *Malpaisomys* appears consistently smaller ($P < 0.001$), as much as 27% smaller than *Aethomys*; the taxon to which it is closest in size (only 3% smaller) is *Oenomys*.

Shape variations were examined using CA1 as a synthetic shape axis (Fig. 6B). A parallel morphologi-

Table 2. Size and shape differentiation among *Malpaisomys* populations. Probabilities produced by a *t*-test on size of first upper molar estimated by A_0 and by MANOVA of the shape of the first upper and lower molars (Wilks' lambda). Significant probabilities in bold

	M1/ Size				M1/ Shape				M1 Shape			
	CCAL	CVA4	CDA	LOB4	CCAL	CVA4	CDA	LOB4	CCAL	CVA4	CDA	LOB4
CCAL	–				–				–			
CVA4	0.007	–			0.314	–			0.001	–		
CDA	0.036	0.461	–		0.180	0.074	–		0.073	0.203	–	
LOB4	0.001	0.000	0.001	–	0.326	0.000	0.002	–	0.005	0.000	0.005	–

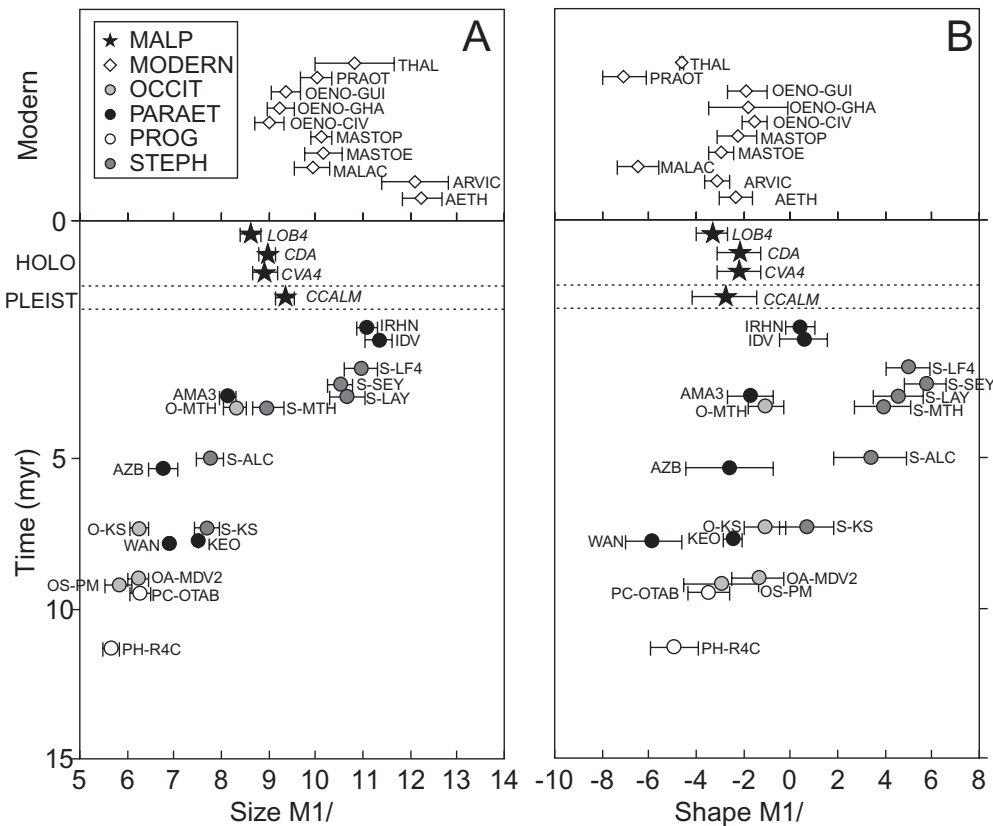


Figure 6. Morphological evolution of the fossil lineages, and comparison with *Malpaisomys* and modern murines. A, size of the first upper molars. B, shape of the first upper molars, estimated by scores on the first canonical axis, representing 46% of the among-group variance. Error bars are ± 1 SD. Symbols per Fig. 3; locality or sample abbreviations per Table 1.

cal trend is displayed in both fossil lineages, but the branch leading to *Stephanomys* shows a more pronounced divergence over time. *Malpaisomys* appears less differentiated than the extreme morphotypes at the end of both lineages (Pleistocene *Paraethomys* and Late Pliocene *Stephanomys*) and is rather close to intermediate morphologies. Considering the modern taxa, *Malacomys* and *Praomys* are the most different from *Malpaisomys*.

EVOLUTIONARY RATES

For size and shape evolutionary rates (Fig. 7A, B), similar log-log linear relationships were observed between time interval and evolutionary rate for both fossil lineages, although no relationship was found for modern taxa (Table 3). Evolutionary rates of size are more dispersed around the general trend, due to the relatively frequent cases of 'stasis' observed for size (observed

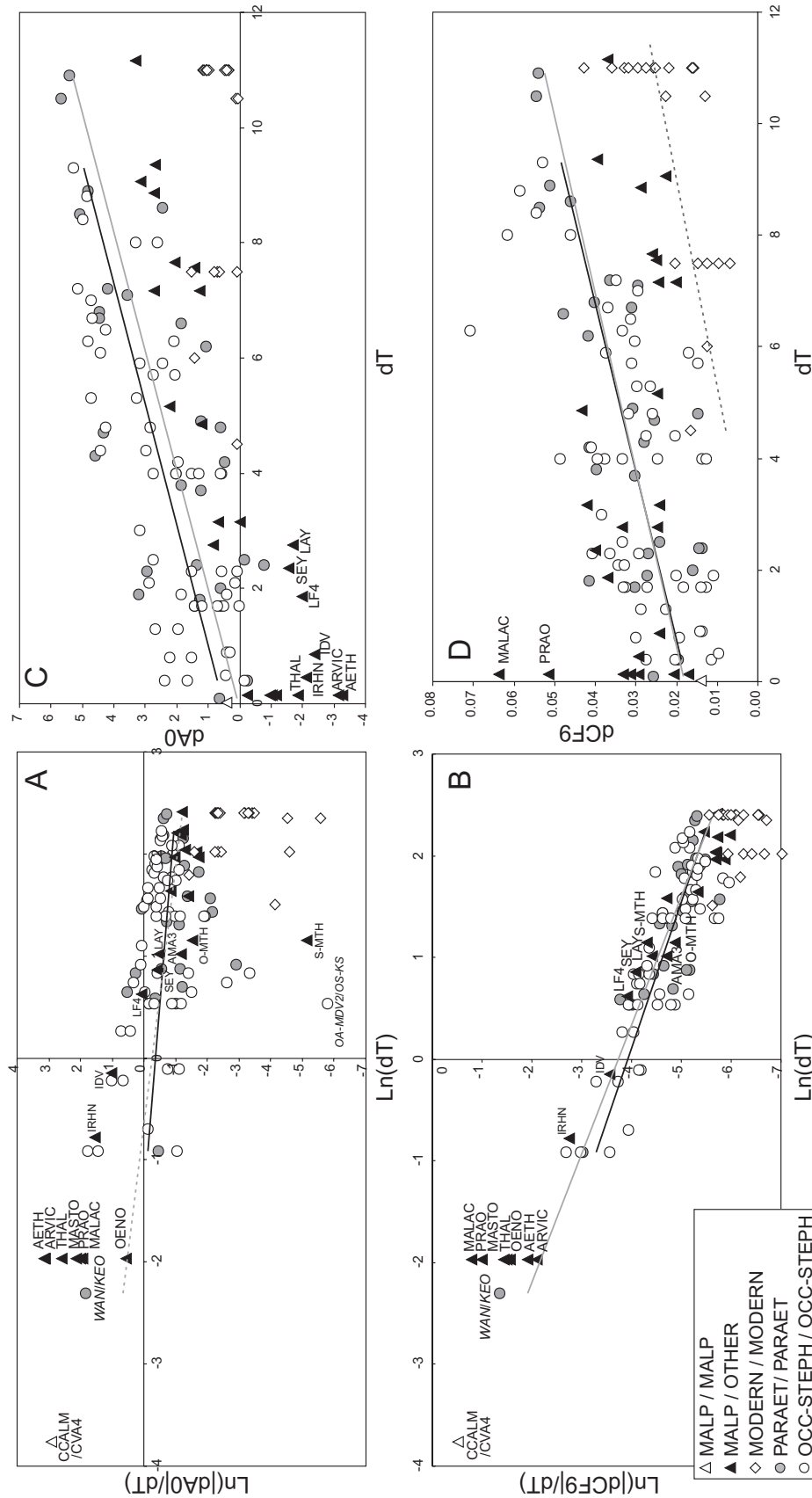


Figure 7. Relationship between time interval and morphological evolution regarding size (A, C) and shape (B, D) of the first upper molars. Size distance is estimated as differences in A_0 , shape distance as the Euclidean distance calculated based on the Fourier coefficients of the first nine harmonics. (A, B) Log-log relationship between evolutionary rates and time interval. (C, D) Relationship between time interval and morphological distance. Lines correspond to a linear regression on the *Occitanomys*/*Stephanomys* lineage (black line), the *Paraethomys* lineage (light grey line), and modern taxa (dark grey line). Dotted lines $P < 0.05$; solid line $P < 0.001$. (▲) pair including *Malpaisomys*; (△) corresponds to the distance between a pair of *Malpaisomys* samples, Costa Calma and CVA4. Locality or sample abbreviations per Table 1.

Table 3. Relationship between time interval and morphological evolution. Coefficient of correlation (R), probability (P) and slope (α) of the linear regression are given. Log of time interval is compared to log-transformed evolutionary rates of size [$\ln(l\ dA_0\ l/dT)$] and shape [$\ln(dCF9/dT)$]. Shape distance is calculated as Euclidean distance between Fourier coefficients of the first nine harmonics (CF9) of the RFT on outlines of the first upper molars. Second, time interval is compared to morphological distances in size (dA_0) or shape ($dCF9$)

	ln(dT)			ln(dT)			dT					
	R	P	α	R	P	α	R	P	α			
MODERN	0.254	0.140	1.217 ± 0.805	-0.181	0.299	-0.316 ± 0.300	0.432	0.010	0.448 ± 0.163	0.346	0.046	0.003 ± 0.001
PARAETH	-0.441	0.019	-0.394 ± 0.157	-0.915	0.000	-0.793 ± 0.068	0.744	0.000	0.468 ± 0.086	0.758	0.000	0.003 ± 0.001
STEPH	-0.599	0.000	-0.606 ± 0.134	-0.837	0.000	-0.695 ± 0.062	0.755	0.000	0.478 ± 0.057	0.609	0.000	0.003 ± 0.001

evolutionary rates largely below the regression line in Fig. 7A). The WAN/KEO pair within the *Paraethomys* lineage appeared as an outlier. This is due to a large morphological change during a short time interval. Differentiation rates derived from the modern taxa and the current molecular phylogenies are in broad agreement with evolutionary rates observed in the fossil record, although they are generally lower.

Rates of evolution calculated for pairs including *Malpaisomys* are highly variable. All the rates calculated between *Malpaisomys* and fossil deposits were close to the regression lines of fossil lineages. In contrast, a hypothesized late colonization by extant taxa during the low sea level of the Late Pleistocene (e.g. at 140 kyr) corresponds to a higher evolutionary rate. The highest rates correspond to a size evolution of *Malpaisomys* from an *Aethomys* or *Arvicanthis*-like ancestor and to a shape evolution from *Malacomys* or *Praomys*. The rate calculated for the Pleistocene and Holocene populations of *Malpaisomys* falls close to the regression lines of the fossil lineages, despite the very short time interval. Still, the uncertainty about possible colonization periods by extant taxa undermines the calculation of evolutionary rates.

Evaluation of evolutionary rates as the slope between time interval and morphological distance should provide a more robust estimate regarding uncertainties concerning the time interval. Significant relationships are found for the shape of modern taxa as well as the fossil lineages (Fig. 7C, D) with similar slopes and thus estimates of evolutionary rates (Table 3). An offset between regression lines involving modern and fossil samples is likely due to a difference in estimating morphological distance and time interval between successive fossil samples and extant coexisting taxa.

The size evolution of *Malpaisomys* from *Aethomys*, *Arvicanthis*, *Thallomys*, Pleistocene *Paraethomys* and Late Pliocene *Stephanomys* (LF4, SEY, LAY) would correspond with major decreases in size never recorded in the fossil lineages. Shape evolution from *Malacomys* or *Praomys* would provide an example of rapid morphological evolution. Our conclusions are in agreement with those based on evolutionary rates (Fig. 7A, B) but seem more robust regarding uncertainties in dating.

DISCUSSION

Our study of the morphological differentiation of the first upper and lower molars of murine rodents of varying diets and phylogenetic backgrounds, and the relationship with the insular *Malpaisomys* produced complex results that necessitate discussion. Other teeth than the first upper and lower molars would have provided valuable complementary infor-

mation. The second upper molar displays some peculiar and informative features, for example regarding the lineage *Paraethomys*. However, the first upper molar frequently overlaps with the second on a molar row, hindering recognition of the outline of the latter and making comparison of second upper molar outlines more problematic for modern and fossil taxa, as the molars of the latter are usually found in isolation. Skeletal features are seldom found intact in the fossil record, hindering a robust morphometric analysis. Published data can nevertheless be discussed in relation to the morphometric results we have obtained based on the first upper and lower molars.

PARALLEL EVOLUTION AND DIVERSIFICATION

The first signal emerging from the morphometric analysis of both the first and upper molars is a clustering of the taxa independent of their phylogenetic origin. This pattern could be related to diet, based on the known or inferred ecology of the taxa. Ecology of modern taxa can be investigated by direct observation, for example, the content of the digestive tract provides evidence of a herbivorous diet for *Oenomys* and an omnivorous diet, with overall low cellulose content, for *Mastomys* and *Praomys* (Dieterlen, 1967). Such direct observations are of course not available for fossil taxa. By comparing them with extant animals, fossil species displaying the highly specialized dental pattern corresponding to stephanodonty have been interpreted as herbivorous.

The clusters observed in the morphological space (Fig. 3) can therefore be interpreted as grades of evolution. One group comprises omnivorous taxa, with a mixture of modern phylogenetic groups (*Mastomys*, *Malacomys*) and primitive fossil forms (*Progonomys*), the second herbivorous taxa, displaying either intermediate stephanodont features or none at all (*Arvicanthis*). The basic dental pattern associated with an omnivorous diet corresponds to a slender, asymmetric outline of the first upper molar. The herbivorous grade is characterized by a broadening of the first upper molar compared to the basic dental pattern. This should be functionally related to an increase in surface of contact between cheek teeth, whether or not stephanodont crests are developed.

The taxa in which stephanodonty reaches its maximum development diverge morphologically from this second cluster. In all three cases (*Oenomys*, Pleistocene *Paraethomys* and Pliocene *Stephanomys*), the morphology corresponds to even broader molars and to a symmetrical outline. The three taxa achieve this morphology in their own, peculiar way, with, for instance, a more developed posterior part in *Oenomys* than in *Stephanomys*.

In both fossil lineages where complete stephanodonty evolved, temporal patterns of evolution are parallel (Fig. 6) and occur at the same rate (Fig. 7). This suggests that evolution might have occurred under similar forces and/or constraints. The similarity of the evolutionary rates also provides a robust estimate of patterns and rates of evolution on the mainland.

RELATIONSHIPS OF *MALPAISOMYS* WITH MAINLAND TAXA

Within this morphological pattern among modern and fossil taxa, *Malpaisomys* clearly falls within the intermediate cluster of herbivorous diet. This supports a palaeoecological interpretation of the taxon as herbivorous, but poses the problem of identifying its mainland ancestor. In particular, herbivory could either be inherited from this ancestor or the result of a parallel evolution on the islands.

Island populations of rodents are known to frequently display an increase in size compared to mainland relatives (Foster, 1964). A decrease in size associated with insular conditions therefore seems unlikely, and is in any event rare in evolutionary lineages (Fig. 7C). Such an interpretation excludes large taxa as being potential ancestors of *Malpaisomys*, especially *Aethomys*, *Arvicanthis*, *Thallomys*, Pleistocene *Paraethomys*, and Late Pliocene *Stephanomys*. Shape, by contrast, reveals a different pattern. Among modern taxa, *Aethomys* (and to a lesser extent, *Arvicanthis*) are the most similar regarding first upper molar shape (Figs 3, 4B) while *Malacomys* and *Praomys* are the most different (Fig. 7D). Some discrepancies exist between the shape of the first upper or lower molars. Based on the upper molars, the extreme stephanodonts *Oenomys*, Pleistocene *Paraethomys* and Pliocene *Stephanomys* appear to be more differentiated than *Malpaisomys*, which would be closest to *Occitanomys* (e.g. O-MTH) or Late Pliocene *Paraethomys* (Fig. 3B). Based on the first lower molar shape, however, *Malpaisomys* appears to be closer to the more derived, Pleistocene *Paraethomys*, while remaining associated with Late Pliocene *Occitanomys* (Fig. 3C). In agreement with our results, the morphological relatedness of the stephanodont genera *Malpaisomys*, *Oenomys* and *Stephanomys* had previously been shown by phenetic distances of dental characters (López-Martínez *et al.*, 1998). Skull characters provide a different picture, suggesting a similarity between *Stephanomys* and *Malpaisomys*, *Oenomys* having been found to be more similar to non-stephanodont genera like *Rattus* (López-Martínez *et al.*, 1998). Mosaic evolution likely occurred due to diverse selective pressures acting on different characters. The skull is more influenced by habitat whereas dental patterns reflect diet. The similarity of the skulls of *Malpai-*

somys and *Stephanomys* may be a consequence of a similar mode of life within a rocky landscape (López-Martínez *et al.*, 1998).

Combining these various results shows that morphologically the taxa closest to *Malpaisomys* are to be found among Pliocene fossil lineages related to either *Paraethomys* or *Occitanomys*. A hypothesized colonization of the eastern Canary Islands by members of these genera minimizes the evolution in both size and shape. A third alternative is colonization by an ancestor of the arvicanthine group, smaller in size than the modern representatives and already displaying a morphology characteristic of the intermediate, herbivorous group. Gene flow between mainland and canarian populations has been promoted by low sea level during glacial periods in some birds (Idaghdour *et al.*, 2004). However, any hypothesis considering such a recent colonization event for *Malpaisomys* would imply extremely high evolutionary rates and reversion in size and/or shape. Morphometric methods favour hypotheses which minimize morphological distance and evolutionary rates. Nonetheless, observations of the fossil lineages (Fig. 7) consistently reveal that such high rates and reversion seldom occur. We therefore favour the hypothesis of an ancient colonization event by a mainland taxon already exhibiting a trend toward herbivory.

Biogeographical considerations should also be considered when evaluating the different hypotheses of colonization. The sea-surface current system around the Canary Islands (Stramma & Siedler, 1988), as well as the dominant trade winds, favour a colonization event from North Africa or the Iberian Peninsula (Fig. 1), providing additional support for a relatively ancient colonization event involving *Paraethomys* or *Occitanomys*. A Late Miocene or Pliocene colonization leading to *Malpaisomys* has been previously suggested (Hutterer *et al.*, 1988; Michaux *et al.*, 1991) and is supported by our results. This hypothesis is not contradicted by dating of the insular volcanic complex, indicating that subaerial areas in the eastern Canary Islands are as old as 15 Myr (Carracedo & Soler, 1995; Ancochea *et al.*, 1996).

DIFFERENTIATION AMONG *MALPAISOMYS* POPULATIONS

After the colonization event, the ancestor of *Malpaisomys* may have evolved into the endemic form within an isolated gene pool. This evolution cannot be tracked in the fossil record because the oldest Pleistocene deposits in the eastern Canary Islands are of *Malpaisomys* rather than an intermediate form. Still, its late evolution during the Pleistocene until its extinction during historical times can be assessed. Preliminary results emerge from the four deposits examined. A

morphological difference is observed between the Pleistocene and the Holocene populations from Fuerteventura (Table 2). During this time interval, *Mus* colonized the islands and began to feature greatly in the deposits (Michaux *et al.*, 1996; Castillo *et al.*, 2001). The invasion of an island by a generalist competitor has been observed to cause a size decrease of the resident species in several small mammals (Yom-Tov, Yom-Tov & Moller, 1999). The size decrease and shape difference among *Malpaisomys* populations may thus document a response to the arrival of the generalist house mouse. Still, the evolutionary rate estimated for this evolution (Fig. 7) does not differ from observations of fossil lineages, suggesting that the new ecological interaction did not trigger an exceptionally rapid morphological evolution.

The population of the islet Lobos (4.6 km²) also differentiated from the Holocene populations in Fuerteventura (1633 km²; Fig. 5), although the presence of *Mus* suggests a similar age. This may document a small-scale insularity effect due to partial genetic isolation.

INSULAR EVOLUTION AND ENVIRONMENTAL FACTORS

It has been suggested that once an island endemic species has evolved to occupy its particular niche, it remains unchanged regardless of changes in climate and vegetation, unless new competitors migrated (Sondaar, 2000). *Malpaisomys* experienced the arrival of *Mus* between the Pleistocene and the Holocene, but the ecological interaction did not trigger an important morphological variation (Figs 5, 7).

Alternatively, major changes in size and shape can be a response to environmental change. A climatic degeneration occurred during the late Pliocene, beginning *c.* 3.5 Mya (Suc *et al.*, 1995; An *et al.*, 2001) and culminating at the Plio-Pleistocene boundary (Thunell *et al.*, 1991). Aridification increased step-wise around 2.8, 1.7 and 1.0 Mya (deMenocal, 2004). The transition between Pliocene and Pleistocene *Paraethomys* can be interpreted as a response to these abiotic variations (Renaud *et al.*, 1999a). The shift in size and shape of the late Pliocene *Stephanomys* may document a similar reaction, although the response to the climatic change would have occurred earlier. The two lineages evolved towards enhanced stephanodonty. Hence, the morphological trend can be interpreted as an adaptive response to changing diet, climate and vegetation.

The morphological differentiation of *Malpaisomys* is limited compared to the extremely divergent late *Paraethomys* and *Stephanomys*. Pleistocene climatic variations had an impact on the Canary Islands as well as on the mainland. Alternate warm and cool phases have been documented in molluscan faunas (Meco *et al.*, 1992, 2002). Local climate could also have been influenced by intensified trade winds and

upwelling of cold waters during glacial times (Hendricks *et al.*, 2002). However, insular climatic variations may also have been mitigated by these oceanic conditions. Fuerteventura nowadays has a warmer and drier climate than the North African mainland (annual average temperature 19.8 vs. 17.5 °C; annual precipitation 245 vs. 570 mm). Seasonal climatic variation is reduced compared to the mainland (monthly temperature difference 8.0 vs. 15.7 °C and monthly precipitation difference 71 vs. 155 mm; summarized from data supplied by the NOAA NCDC GPCP monthly stations). The reduction in environmental variation and ecological interaction on the Canary Islands may have favoured a relative morphological stability of *Malpaisomys*. On the mainland, *Paraethomys* and *Stephanomys* would have experienced an important morphological evolution because of the cumulative effect of climate forcing and species interactions.

The relative morphological stability of *Malpaisomys* compared to mainland fossil and modern extreme forms does not support a hypothesis of higher rates of morphological evolution on islands due to a change in genetic background following the founder effect, repeated bottlenecks and genetic drift (Berry, 1973). It rather supports the view of insular endemics as relicts of extinct, mainland populations (Cronk, 1992). Furthermore, gigantism, which is supposed to be a feature typical of insular rodent populations (Foster, 1964), did not occur in *Malpaisomys*. This taxa is characterized by a small size compared to various modern, late Pliocene and Pleistocene taxa (Fig. 6A). On the contrary, other murine endemics from the western Canary Islands were giant rats: *Canariomys bravoii* on Tenerife and *C. tamarani* on Gran Canaria, both now extinct (Crusafont & Petter, 1964; López-Martínez & López-Jurado, 1987; Michaux *et al.*, 1996).

The discrepancy between these patterns of size evolution, leading to either giant rats or a rodent not larger than a big mouse, requires explanation. A high proportion of endemic species is often associated with ancient islands on the continental shelf, as well as with large, elevated volcanic islands in tropical and warm-temperate latitudes, due to the large variety of habitats. Smaller, less elevated islands have a lower proportion of endemics (Whittaker, 1998). The giant rats *Canariomys* occurred on the elevated volcanic islands of the Canary Archipelago (Tenerife 3718 m, Gran Canaria 1949 m). On the other hand, *Malpaisomys* is characteristic of the low-lying eastern Canary Islands (Fuerteventura 807 m, Lanzarote 670 m), likely offering a reduced variety of habitats. The abiotic difference between eastern and western Canary Islands could also have caused variations in biotic interactions, causing in turn various size responses of the rodents. Predation may strongly constrain size evolution of small

mammals on islands. Size increase in insular wood mice (*Apodemus sylvaticus*) is favoured by both a reduced island area and a lower number of predator species (Michaux *et al.*, 2002). The predation pressure of the barn owl on *Malpaisomys* (Castillo *et al.*, 2001) may have been enhanced by the lack of dense forest cover on the eastern Canary Islands. Small size would have been selected for, because it would have allowed *Malpaisomys* to escape predation by hiding in fissures. Its unusual habitat of cavities in recent lava flows is further supported by skeletal characteristics (Boye *et al.*, 1992). On the other hand, the dense vegetation cover in most parts of Tenerife and Gran Canaria would have offered easy shelter to *Canariomys*, allowing for larger size despite predation.

CONCLUSIONS

1. Morphometric comparison of the first upper and lower molars in several modern and fossil taxa allowed the investigation of the potential influence of phylogeny and ecology on dental morphology. In the morphometric space, clusters of taxa are observed, corresponding to slender, asymmetrical outlines, distinct from broader and more symmetrical shapes. These clusters can be related to difference in diet, with omnivorous taxa separated from more herbivorous ones. The pattern emerging from the morphometric analysis can be interpreted as grades of evolution reached independently by different phylogenetic groups. Some highly specialized taxa have further diverged from the herbivorous cluster and from each other, combining a phylogenetic and ecological signal. Evolution in both fossil lineages occurred at similar rates and was parallel over time.
2. The extinct lava mouse from the Eastern Canary Islands, *Malpaisomys insularis*, is associated with intermediate morphotypes characterized by a herbivorous diet.
3. Decrease in size seems unlikely in insular rodents, which generally tend to increase in size. A recent colonization event by modern representatives appears unlikely, because they are larger than *Malpaisomys*. Pleistocene *Paraethomys* and Late Pliocene *Stephanomys* also became large and morphologically very different from *Malpaisomys*. Based on size and shape similarity, morphometrics favours a Pliocene colonization event by a *Paraethomys* or *Occitanomys*-like ancestor.
4. Shape differentiation of *Malpaisomys* is also of limited importance compared to the directional evolutionary trends observed in the *Paraethomys* and *Stephanomys* mainland lineages during the Late Pliocene or Early Pleistocene. The morphological stability of *Malpaisomys* might have been due to

reduced interactions among competitor species, compared to the situation pertaining on the mainland, where continual interactions among rodent species could have reinforced the effects of climatic constraints. The absence of insular gigantism may further be due to predation pressure, favouring animals of small size able to hide in fissures of recent lava flows.

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REFERENCES

- Aguilar J-P, Berggren WA, Aubry M-P, Kent DV, Clauzon G, Benammi M, Michaux J. 2004.** Mid Neogene Mediterranean marine-continental correlations: An alternative interpretation. *Palaeogeography, Palaeoclimatology, Palaeoecology* **204**: 165–186.
- Aguilar J-P, Crochet J-Y, Hebrard O, Le Strat P, Michaux J, Pedra S, Sigé B. 2002.** Les micromammifères de Mas Rambault 2, gisement karstique du Pliocène supérieur du Sud de la France: âge, paléoclimat, géodynamique. *Géologie de la France* **4**: 17–37.
- An Z, Kutzbach JE, Prell WL, Porter SC. 2001.** Evolution of Asian monsoons and phased uplift of the Himalaya-Tibetan plateau since Late Miocene times. *Nature* **211**: 62–66.
- Ancochea E, Brändle JL, Cubas CR, Hernán CR, Huertas MJ. 1996.** Volcanic complexes in the eastern ridge of the Canary Islands: the Miocene activity of the islands of Fuerteventura. *Journal of Volcanology and Geothermal Research* **70**: 183–204.
- Benammi M, Calvo M, Prévot M, Jaeger J-J. 1996.** Magnetostratigraphy and paleontology of Aït Kandoula Basin (High Atlas, Morocco) and the African-European late Miocene terrestrial fauna exchanges. *Earth and Planetary Science Letters* **145**: 15–29.
- Benammi M, Orth B, Vianey-Liaud M, Chaimanee Y, Suteethorn V, Feraud G, Hernandez J, Jaeger J-J. 1995.** Micromammifères et biochronologie des formations néogènes du flanc sud du Haut-Atlas Marocain: implications biogéographiques, stratigraphiques et tectoniques. *Africa Geoscience Review* **2**: 279–310.
- Berry RJ. 1973.** Chance and change in British Long-tailed field mice (*Apodemus sylvaticus*). *Journal of Zoology, London* **170**: 351–366.
- Boye P, Hutterer R, López-Martínez N, Michaux J. 1992.** A reconstruction of the Lava mouse (*Malpaisomys insularis*), an extinct rodent of the Canary Islands. *Zeitschrift für Säugetierkunde* **57**: 29–38.
- Carracedo JC, Soler V. 1995.** Anomalously shallow palaeomagnetic inclinations and the question of the age of the Canarian Archipelago. *Geophysical Journal International* **122**: 393–406.
- Castillo C, Martín-González E, Coello JJ. 2001.** Small vertebrate taphonomy of La Cueva del Llano, a volcanic cave on Fuerteventura (Canary Islands, Spain). Palaeoecological implications. *Palaeogeography, Palaeoclimatology, Palaeoecology* **166**: 277–291.
- Chevret P. 1994.** Etude évolutive des Murinae (Rongeurs: Mammifères) africains par hybridation ADN/ADN. Comparaisons avec les approches morphologiques et paléontologiques. Thèse, Université Montpellier II.
- Chevret P, Denys C, Jaeger J-J, Michaux J, Catzeflis F. 1993.** Molecular evidence that the spiny mouse (*Acomys*) is more closely related to gerbils (Gerbillinae) than to true mice (Murinae). *Proceedings of the National Academy of Sciences, USA* **90**: 3433–3436.
- Chevret P, Michaux J, Catzeflis F. 2001.** Phylogénie moléculaire des Murinae: Implications systématiques et biogéographiques. In: *Systématique et Biogéographie Journées 2001*. Paris: Société Française de Systématique.
- Coiffait B. 1991.** Contribution des rongeurs du Néogène d'Afrique à la biostratigraphie d'Afrique du Nord Occidentale. Thèse, Université Nancy I.
- Cordy J-M. 1978.** Caractéristiques générales de la microévolution du genre *Stephanomys* (Rodentia, Muridae). *Bulletin de la Société Géologique de France* **XX**: 815–819.
- Cronk QCB. 1992.** Relict floras of Atlantic islands: patterns assessed. *Biological Journal of the Linnean Society* **46**: 91–103.
- Crusafont M, Petter F. 1964.** Un muriné géant fossile des Iles Canaries *Canariomys bravoii* gen. nov., sp. nov. (Rongeurs, Muridés). *Mammalia* **28**: 608–611.
- van Dam JA. 1997.** The small mammals from the upper Miocene of the Teruel-Alfambra region (Spain): paleobiology and paleoclimatic reconstructions. *Geologica Ultraiectina* **156**: 1–204.
- van Dam J, Alcalá L, Alonzo Zarza AM, Calvo JP, Garcés M, Krijgsman W. 2001.** The upper Miocene mammal record from the Teruel-Alfambra region (Spain). The MN system and continental stage/age concept discussed. *Journal of Vertebrate Paleontology* **21**: 367–385.
- Denys C. 1994.** Diet and dental morphology of two coexisting *Aethomys* species (Rodentia, Mammalia) in Mozambique. Implications for diet reconstruction in related extinct species from South Africa. *Acta Theriologica* **39**: 357–364.
- Denys C, Michaux J. 1992.** La troisième molaire supérieure chez les Muridae d'Afrique tropicale et le cas des genres *Acomys*, *Uranomys* et *Lophuromys*. *Bonner Zoologische Beiträge* **43**: 367–382.

- Dieterlen F. 1967.** Ökologische Populationsstudien an Muriden des Kivugebietes (Congo). Teil I. *Zoologisches Jahrbuch Abteilung für Systematik, Ökologie und Geographie der Tiere* **94**: 369–426.
- Ducroz JF, Volobouev V, Granjon L. 2001.** An assessment of the systematics of the Arvicanthine rodents using mitochondrial DNA sequences: evolutionary and biogeographical implications. *Journal of Mammalian Evolution* **8**: 173–206.
- Foster JB. 1964.** Evolution of mammals on islands. *Nature* **202**: 506–521.
- Hendericks J, Freudenthal T, Meggers H, Nave S, Abrantes F, Bollmann J, Thierstein HR. 2002.** Glacial-interglacial variability of particle accumulation in the Canary Basin: a time-slice approach. *Deep-Sea Research II* **49**: 3675–3705.
- Hutterer R, López-Martínez N, Michaux J. 1988.** A new rodent from the quaternary deposits of the Canary Islands and its relationships with Neogene and recent murids of Europe and Africa. *Palaeovertebrata* **18**: 241–262.
- Idaghdour Y, Broderick D, Korrida A, Chbel F. 2004.** Mitochondrial control region diversity of the houbara bustard *Chlamydotis undulata* complex and genetic structure along the Atlantic seaboard of North Africa. *Molecular Ecology* **13**: 43–54.
- Jaeger J-J. 1977.** Les rongeurs du Miocène moyen et supérieur du Maghreb. *Paleovertebrata* **8**: 1–166.
- 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. *Comptes Rendus de l'Académie des Sciences Paris, Série D* **280**: 1673–1676.
- Lomolino MV. 1985.** Body size of mammals on islands: the island rule reexamined. *American Naturalist* **125**: 310–316.
- López-Martínez N, López-Jurado LF. 1987.** *Un nuevo murido gigante del Cuaternario de Gran Canaria. Canariomys tamarani* nov. sp (Rodentia mamalia). Sevilla: Estación Biológica de Doñana, 59.
- López-Martínez N, Michaux J, Hutterer R. 1998.** The skull of *Stephanomys* and a review of *Malpaisomys* relationships (Rodentia: Muridae): taxonomic incongruence in murids. *Journal of Mammalian Evolution* **5**: 185–215.
- Manly BFJ. 1994.** *Multivariate statistical methods. A primer*, 2nd edn. London: Chapman & Hall.
- Mayr E. 1954.** Change of genetic environment and evolution. In: Huxley JS, Hardy AC, Ford EB, eds. *Evolution as a process*. London: Allen & Unwin, 156–180.
- Meco J, Guillou H, Carracedo JC, Lomoschitz A, Ramos A-J, Rodríguez-Yáñez J-J. 2002.** The maximum warmings of the Pleistocene world climate recorded in the Canary Islands. *Paleogeography, Palaeoclimatology, Palaeoecology* **185**: 197–210.
- Meco J, Petit-Maire N, Reyss J-L. 1992.** Le Courant des Canaries pendant le stade isotopique 5, d'après la composition faunistique d'un haut niveau marin à Fuerteventura (28°N). *Comptes Rendus de l'Académie des Sciences, Série II* **314**: 203–208.
- deMenocal PB. 2004.** African climate and faunal evolution during the Pliocene-Pleistocene. *Earth and Planetary Science Letters* **220**: 3–24.
- Michaux J. 1971.** Muridae (Rodentia) néogènes d'Europe sud-occidentale. Evolution et rapports avec les formes actuelles. *Paléobiologie Continentale, Montpellier II* (1): 1–67.
- Michaux J. 1978.** Les muridés actuels et fossiles. In: Bons J, ed. Aspects modernes des recherches sur l'évolution. *Mémoires et Travaux de l'Institut de Montpellier, EPHE* **1**: 133–143.
- Michaux JR, Goüy de Bellocq J, Sara M, Morand S. 2002.** Body size increase in rodent populations: a role for predators? *Global Ecology and Biogeography* **11**: 427–436.
- Michaux J, Hutterer R, López-Martínez N. 1991.** New fossil faunas from Fuerteventura, Canary Islands: evidence for a Pleistocene age of endemic rodents and shrews. *Comptes Rendus de l'Académie des Sciences, Série II* **312**: 801–806.
- Michaux J, López-Martínez N, Hernández-Pacheco J-J. 1996.** A ¹⁴C dating of *Canariomys bravoii* (Mammalia Rodentia), the extinct giant rat from Tenerife (Canary islands, Spain), and the recent history of the endemic mammals in the archipelago. *Vie et Milieu* **46**: 261–266.
- Misonne X. 1969.** *African and Indo-Australian Muridae: evolutionary trends*. Tervuren: Musée Royal de l'Afrique Centrale.
- Montgelard C. 1992.** Albumin preservation in fossil bones and systematics of *Malpaisomys insularis* (Muridae, Rodentia), an extinct rodent of the Canary Island. *Historical Biology* **6**: 293–302.
- Pergams ORW, Ashley MV. 2001.** Microevolution in island rodents. *Genetica* **112–113**: 245–256.
- Renaud S. 1999.** Size and shape variability in relation to species differences and climatic gradients in the African rodent *Oenomys*. *Journal of Biogeography* **26**: 857–865.
- Renaud S, Benammi M, Jaeger J-J. 1999a.** Morphological evolution of the murine rodent *Paraethomys* in response to climatic variations (Mio-Pleistocene of North Africa). *Paleobiology* **25**: 369–382.
- Renaud S, Michaux J, Mein P, Aguilar J-P, Auffray J-C. 1999b.** Patterns of size and shape differentiation during the evolutionary radiation of the European Miocene murine rodents. *Lethaia* **32**: 61–71.
- Renaud S, Millien V. 2001.** Intra- and interspecific morphological variation in the field mouse species *Apodemus argenteus* and *A. speciosus* in the Japanese archipelago: the role of insular isolation and biogeographic gradients. *Biological Journal of the Linnean Society* **74**: 557–569.
- Renaud S, van Dam J. 2002.** Influence of biotic and abiotic environment on dental size and shape evolution in a Late Miocene lineage of murine rodents (Teruel Basin, Spain). *Palaeogeography, Palaeoclimatology, Palaeoecology* **184**: 161–173.
- Rohlf FJ. 1998.** *NTSYSpc. Numerical taxonomy and multivariate analysis system*, 2.02. New York: Exeter Software.
- Schaub S. 1938.** Tertiäre und Quartäre Murinae. *Abhandlungen der Schweizerischen Paleontologischen Gesellschaft, Basel* **61**: 1–39.
- Schluter D. 2000.** *The ecology of adaptive radiation*. Oxford

- Series on Ecology and Evolution. Oxford: Oxford University Press.
- Sondaar PY. 2000.** Early human exploration and exploitation of islands. *Tropics* **10**: 203–230.
- Stramma L, Siedler G. 1988.** Seasonal changes in the North Atlantic subtropical gyre. *Journal of Geophysical Research* **93**: 8111–8118.
- Suc J-P, Bertini A, Combourieu Nebout N, Diniz F, Leroy S, Russo-Ermolli E, Zheng Z, Bessais E, Ferrier J. 1995.** Structure of West Mediterranean vegetation and climate since 5.3 ma. *Acta Zoologica Cracovica* **38**: 3–16.
- Thunell R, Rio D, Sprovieri R, Vergnaud Grazzini C. 1991.** An overview of the post-Messinian paleoenvironmental history of the western Mediterranean. *Paleoceanography* **6**: 143–164.
- van de Weerd A. 1976.** Rodent faunas of the Mio-Pliocene continental deposits of the Teruel-Alfambra region, Spain. *Utrecht Micropaleontology Bulletin, Special Publication* **2**: 1–217.
- Whittaker RJ. 1998.** *Island biogeography. Ecology, evolution and conservation*. Oxford: Oxford University Press.
- Yom-Tov Y, Yom-Tov S, Moller H. 1999.** Competition, coexistence, and adaptation amongst rodent invaders to Pacific and New Zealand islands. *Journal of Biogeography* **26**: 947–958.