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Morphological evolution, ecological diversification and climate change in rodents

Sabrina Renaud[1,*], Jacques Michaux[2,3], Daniela N. Schmidt[4], Jean-Pierre Aguilar[2], Pierre Mein[1] and Jean-Christophe Auffray[2]

[1] *UMR 5125 CNRS 'Paléoenvironnements et Paléobiosphère', Université Claude Bernard Lyon 1, 69622 Villeurbanne, France*
[2] *Institut des Sciences de l'Evolution (CC064), UMR 5554, Université Montpellier 2, 34095 Montpellier Cedex 05, France*
[3] *Laboratoire de Paléontologie des Vertébrés de l'EPHE, Université Montpellier 2, 34095 Montpellier Cedex 05, France*
[4] *Department of Geology, Royal Holloway University of London, Egham TW20 0EX, UK*

Among rodents, the lineage from *Progonomys hispanicus* to *Stephanomys* documents a case of increasing size and dental specialization during an approximately 9 Myr time-interval. On the contrary, some contemporaneous generalist lineages like *Apodemus* show a limited morphological evolution. Dental shape can be related to diet and can be used to assess the ecological changes along the lineages. Consequently, size and shape of the first upper molar were measured in order to quantify the patterns of morphological evolution along both lineages and compare them to environmental trends. Climatic changes do not have a direct influence on evolution, but they open new ecological opportunities by changing vegetation and allow the evolution of a specialist like *Stephanomys*. On the other hand, environmental changes are not dramatic enough to destroy the habitat of a long-term generalist like *Apodemus*. Hence, our results exemplify a case of an influence of climate on the evolution of specialist species, although a generalist species may persist without change.

Keywords: Murinae; evolution; morphometrics; Fourier; shape; climate

1. INTRODUCTION

Competing hypotheses have been proposed to explain long-term evolutionary trends in the fossil record including mammals involving the climate (Stenseth & Maynard Smith 1984) or biotic interactions (Van Valen 1973). Alroy *et al.* (2000) concluded that there is little evidence of climate-forcing on mammalian evolution. Jernvall & Fortelius (2002) provided a different view, with evidence for a link between the drying climate of Europe during the Neogene and evolution of hypsodonty in mammals. A first prerequisite to address this question is a well-preserved fossil group with well-assessed ecology and phylogeny and a time period with major climatic variations. The well-documented evolution of large mammal faunas during the Neogene has consequently been discussed in the context of climate change (Thenius 1951; Crusafont Pairo 1965; Tobien 1967). More recently, similar interpretations have been made for small mammals (van der Meulen & Daams 1992; Reumer 1995). A second prerequisite is to avoid any circular reasoning using environmental data extracted from the same fauna to interpret change in long-term trends in a lineage. We will investigate the relationship between the major climatic changes of the Late Neogene with the evolution of a group of small mammals, the murine rodents (Murinae, Rodentia). The evolutionary patterns observed will be compared with estimates of the major climatic changes based on paleoenvironmental records independent of the mammals.

Murine rodents diversified in Europe around 11.5 Myr ago from primitive forms, *Progonomys cathalai* and *Progonomys hispanicus* (Renaud *et al.* 1999). The former evolved into lineages related to *Apodemus* still living in Europe today (Michaux *et al.* 1997). *P. hispanicus* founded a lineage which developed a peculiar dental specialization termed stephanodonty (Schaub 1938). Ancestral murine rodents as well as modern omnivorous–granivorous taxa share a basic dental pattern characterized by three longitudinal rows of cusps linked by crests to form three transversal chevrons (transverse row of cusps) on the upper molars (*P. hispanicus* in figure 1). *Occitanomys* (*O. sondaari* in figure 1) constitutes an intermediate stage of evolution. The derived *Stephanomys* (*S. donnezani* in figure 1) display more developed longitudinal crests connecting the transverse chevrons on the upper molars. Accompanying these changes in the dental pattern, crowns become larger and higher because of the swelling of the cusps, leading to an occlusal surface with more pronounced ridges and gutters. This specialization has been interpreted as an adaptation to a more abrasive diet, probably grass, by comparison with extant African murines such as *Oenomys* and *Aethomys* (Dieterlen 1967; Michaux 1977; Denys 1994).

This lineage was especially abundant in southwestern European faunas and has been described as an example of phyletic gradualism on the basis of progressive size increase and change in the dental pattern (Gmelig Meyling & Michaux 1973; van de Weerd 1976; Cordy 1978; Bachelet & Castillo Ruiz 1990; van Dam 1996, 1997). The material derives from France and Spain and documents the evolution of the lineage from the ancestral *P. hispanicus* (~11.5 Myr ago) to the latest *Stephanomys*

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* Author for correspondence (sabrina.recaud@univyon1.fr).

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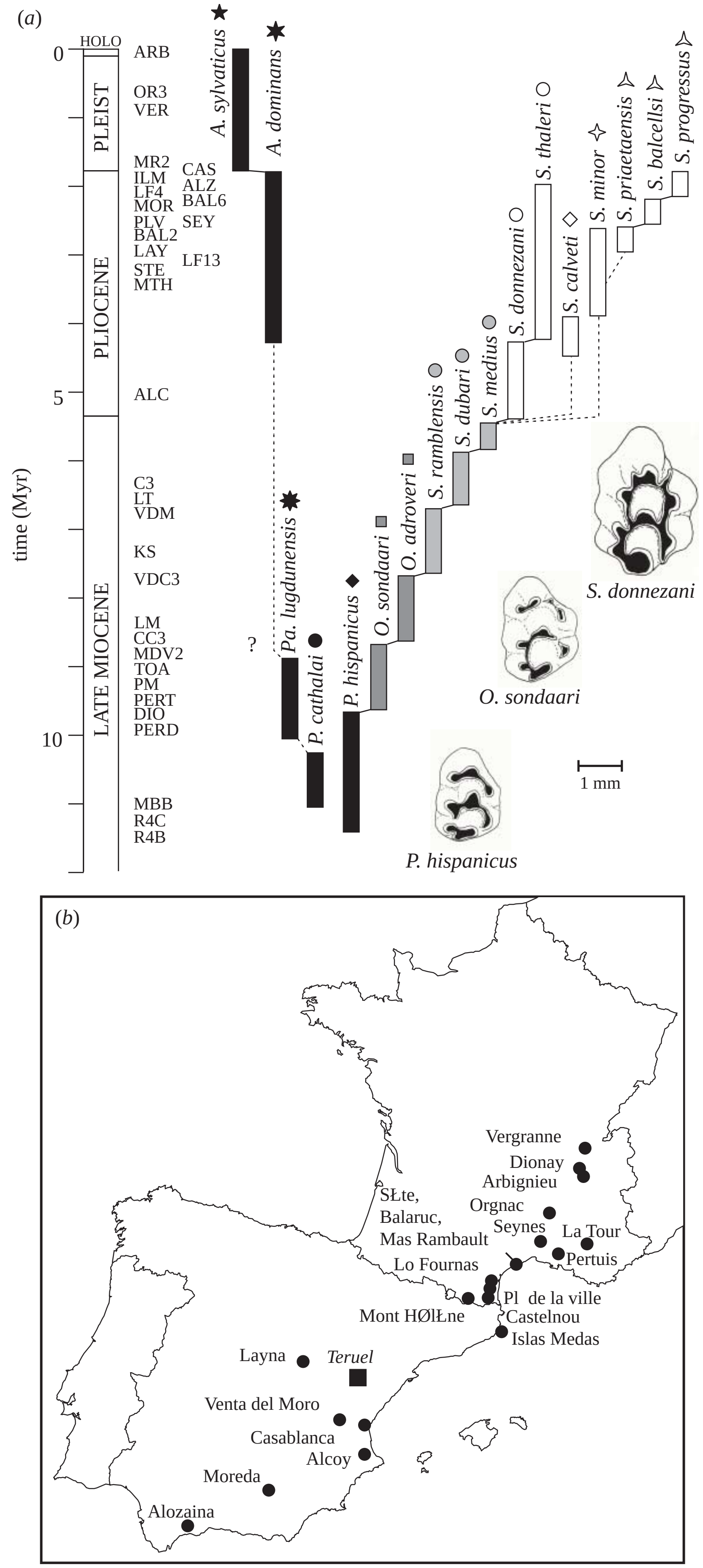

Figure 1. (*a*) Phylogeny of the lineages *P. hispanicus–Stephanomys* and *P. cathalai–Apodemus sylvaticus*. Codes for the deposits in table 1. Full line: agreed ancestor–descendent relationship; dashed line: proposed relationship. Schematic occlusal patterns of upper first molars (inner/lingual side to the right) shown for different stages of the *Stephanomys* lineage. (*b*) Map of the fossil deposits.

Table 1. Deposits with corresponding abbreviation (code), ages in Myr (Age$_C$) based on the correlation proposed by Aguilar *et al.* (2004) and interpolated ages (Age$_I$) based on this calibration and the succession order, number of first upper molars measured (M1).
(In brackets, country: FR, France; SP, Spain. A star indicates a deposit from the Teruel Basin. Below line, modern rodents with country of trapping. Period: MIO, Miocene; PLIO, Pliocene; PLEI, Pleistocene; HOL, Holocene; MOD, modern.)

deposit	period	code	age$_C$	age$_I$	genus	species	M1
La Roma 4B (SP*)	MIO	R4B		11.4	*Progonomys*	*hispanicus*	4
La Roma 4C (SP*)	MIO	R4C		11.3		*hispanicus*	8
Masia del Barbo 2B (SP*)	MIO	MBB	11	11		*hispanicus*	20
						cathalai	6
Peralejos D (SP*)	MIO	PERD		9.7		*hispanicus*	20
Dionay (FR)	MIO	DIO		9.6		*hispanicus*	15
					Parapodemus	*lugdunensis*	24
Pertuis (FR)	MIO	PERT	9.5	9.5	*Occitanomys*	*sondaari*	5
Puente Minero (SP*)	MIO	PM		9.2		*sondaari*	20
Tortajada A (SP*)	MIO	TOA		9.1		*sondaari*	20
Masada del Valle 2 (SP*)	MIO	MDV2	9	9		*adroveri*	20
Concud 3 (SP*)	MIO	CC3		8.7		*adroveri*	20
Los Mansuetos (SP*)	MIO	LM	8.5	8.5		*adroveri*	19
Valdecebro 3 (SP*)	PLIO	VDC3	8/7.5	7.7	*Stephanomys*	*ramblensis*	21
Las Casiones (SP*)	PLIO	KS	7.5/7	7.3		*ramblensis*	20
Venta del Moro (SP)	PLIO	VDM	7/6.5	6.7		*ramblensis*	14
La Tour (FR)	PLIO	LT	6.5/6	6.5		*dubari*	5
Castelnou 3 (FR)	PLIO	C3	6.5/6	6.4		*dubari*	15
Alcoy (SP)	PLIO	ALC		5		*medius*	2
Mont Hélène (FR)	PLIO	MTH	3.3	3.3		*donnezani*	30
					Apodemus	*dominans*	40
Sète (FR)	PLIO	STE	3.0	3.1	*Stephanomys*	*donnezani*	30
					Apodemus	*dominans*	39
Lo Fournas 13 (FR)	PLIO	LF13	3.0	3	*Stephanomys*	*donnezani*	30
Layna (SP)	PLIO	LAY		2.9		*donnezani*	30
Balaruc 2 (FR)	PLIO	BAL2	2.7	2.7		*calveti*	30
					Apodemus	*dominans*	43
Plà de la Ville (FR)	PLIO	PLV	2.5/2.4	2.5	*Stephanomys*	*calveti*	30
					Apodemus	*dominans*	10
Seynes (FR)	PLIO	SEY	2.5/2.4	2.5	*Stephanomys*	*thaleri*	30
					Apodemus	*dominans*	20
Moreda 1B (SP)	PLIO	MOR	2.5/2.3	2.4	*Stephanomys*	*minor*	30
				2.4		*thaleri*	3
Balaruc 6 (FR)	PLIO	BAL6	2.3	2.3		*thaleri*	30
Lo Fournas 4 (FR)	PLIO	LF4		2		*thaleri*	30
Alozaina (SP)	PLIO	ALZ		1.9		*minor*	14
				1.9		*prietaensis*	30
Islas Medas (SP)	PLIO	ILM		1.85		*balcellsi*	30
Casablanca 1 (SP)	PLIO	CAS	1.8	1.8		*progressus*	30
Mas Rambault 2 (FR)	PLIO	MR2		1.7		*thaleri*	2
Vergranne (FR)	PLEI	VER	0.4–0.5	0.45	*Apodemus*	*sylvaticus*	13
Orgnac 3 (FR)	PLEI	OR3	0.35	0.35	*Apodemus*	*sylvaticus*	8
Arbignieu (FR)	HOL	ARB		0.01	*Apodemus*	*sylvaticus*	15
RCA	MOD	AETHH			*Aethomys*	*hindei*	5
Germany	MOD	AS-GER			*Apodemus*	*sylvaticus*	54
Ivory Coast, Senegal	MOD	ARVIC			*Arvicanthis*	sp.	2
Ivory Coast	MOD	OENO-CIV			*Oenomys*	*ornatus*	5
Ghana	MOD	OENO-GHA					4
Guinea	MOD	OENO-GUI					23
Equatorial Guinea	MOD	PRAOT			*Praomys*	*tullbergi*	6
Angola, Somalia	MOD	THAL			*Thallomys*	sp.	2

before its extinction close to the Plio-Pleistocene boundary (table 1). To compare the evolution of dental specialization in *Stephanomys* with a lineage where the primitive pattern was conserved, material documenting the evolution from *P. cathalai* to the modern *Apodemus* has also been analysed. A synthetic phylogeny of the lineages (figure 1) can be proposed based on the literature (Cordy 1978; Bachelet & Castillo Ruiz 1990; Aguilar *et al.* 1993; Aguilar & Michaux 1996; Martín-Suárez & Mein 1998).

2. PATTERNS OF MORPHOLOGICAL DIFFERENTIATION

(a) *Material*

The present study includes data from 875 first upper molars (M1) attributed to three genera and 13 species along the lineage of *Stephanomys* and three genera and four species in the lineage related to *Apodemus* (table 1). Several alluvial, lacustrian and karstic deposits in Spain and France delivered the material measured in this study (figure 1). Order of succession of the deposits has been established using biochronology and magnetostratigraphy (van Dam 1997; Aguilar *et al.* 2004). A calibration to an absolute geological time-scale is still debated (Aguilar *et al.* 2004), but provides indicative numerical ages.

Teeth from a set of modern rodents (Museum d'Histoire Naturelle, Paris) of known diet were measured for comparison: the African rodents *Praomys* (omnivorous), *Aethomys*, *Arvicanthis* and *Thallomys* (herbivorous), *Oenomys* (herbivorous, with specialized stephanodont teeth). Molars of the modern *Apodemus sylvaticus* (omnivorous–granivorous) were measured on a sample of animals from Germany (Institut für Haustierkunde, Kiel).

(b) *Outline analysis*

The outline of the tooth registers the differences in the relative position and importance of the main cusps and hence, is appropriate to describe the overall morphology of the first upper molars in murine rodents. Outline analysis has been used successfully to analyse parts of the investigated lineage (Renaud *et al.* 1996, 1999; Renaud & van Dam 2002).

The outline corresponds to the two-dimensional projection of the tooth viewed from the occlusal surface (top view), with focus at the base of the crown. The starting point was defined as the maximum of curvature at the top of the molar. A radial Fourier transform (RFT; Renaud & Michaux 2003) was performed on the x, y coordinates of 64 equidistant points along the outline. The distance from each point to the centre of gravity of the outline (i.e. radius) was calculated. The variation of the radius along the outline can be approximated by a finite sum of trigonometric functions of decreasing wavelength (the harmonics). The trigonometric function corresponding to each harmonic is characterized by two Fourier coefficients A_n and B_n. The zeroth harmonic A_0 is proportional to the size of the specimen. All other Fourier coefficients are standardized by the zeroth harmonic, in order to eliminate isometric size effects and to concentrate on shape information only. A study on related rodents (Renaud *et al.* 1999) showed that using the first nine harmonics for the first upper molar offers a good compromise between measurement error, information content, and number of variables to be considered.

(c) *Statistical analysis*

For each first upper molar, a set of 18 variables (two coefficients per nine harmonics) was obtained. Multivariate analyses of variance (MANOVA) were performed on this dataset, in order to evaluate the importance of the among-group differentiation relatively to within-group variation. The grouping factor was the species per locality. A test for significance of among-group differences (Wilks' Lambda test) is provided. Associated with the MANOVA, canonical axes are estimated, which can be considered as synthetic shape axes (Manly 1994).

(d) *Morphological differentiation of the first upper molars*

A first analysis included modern and fossil taxa. The grouping factor in the MANOVA was the species per locality for fossil deposits and the species (and country for *Oenomys*) for modern animals. Morphological differentiation of the first upper molars is significant among the different samples ($p<0.001$). The first two canonical axes explain most of the variation (70% of the among-group variance) and are the only axes explaining more than 10% of variance. The first axis (CA1), by far the most important (58.5%), displays a trend corresponding to the temporal ordination of the *Stephanomys* fossil lineage (figure 2). Primitive samples plot toward negative values and are characterized by a slender and asymmetrical outline. Modern taxa also segregate along this axis according to their diet. Omnivorous–granivorous rodents, exemplified by *Praomys* and *Apodemus*, fall within the range of the primitive *Progonomys* along CA1. The more herbivorous *Aethomys*, *Arvicanthis* and *Thallomys* are shifted toward more positive values corresponding to the range of *Occitanomys*. *Oenomys*, characterized by a herbivorous diet and a stephanodont dental pattern, is further shifted toward positive values and ranges with the oldest *Stephanomys* along CA1. This trend corresponds to broader and more symmetrical molars. The broadening of the outline is owing to a swelling of the cusps, increasing the surface of contact between upper and lower cheek teeth and hence increasing the grinding efficiency. The second axis (CA2, 11.8% of variance) displays an offset between the fossil and the modern taxa. It further expresses a late diversification within the Pliocene *Stephanomys*. It seems to correspond to a more pointed posterior part of the tooth, expressing higher crown with tilted cusps that appear as prominent on the outline.

Shape evolution (figure 3*a*) has been evaluated by a second MANOVA focused on the lineages leading to *Stephanomys* on the one hand, and to *Apodemus* on the other hand. Shape differentiation is still highly significant ($p<0.0001$). Evolution along the *Stephanomys* lineage is characterized by brief periods of accelerated change, although the general picture is of a gradual change towards broad and symmetrical upper molars with swollen cusps. A first trend can be recognized from the oldest *P. hispanicus* (~11.5 Myr) to *Occitanomys adroveri* (~8.5 Myr). An important morphological step marks the appearing of *Stephanomys* (~8 Myr). By 5 Myr, *Stephanomys* has reached extremely broad molars associated with achieved stephanodonty. The subsequent shape evolution associated with the Late Pliocene diversification of *Stephanomys* involves characters independent of those expressed along CA1 (cf. figure 2). On the other hand, the lineage related to *Apodemus*, leading from *P. cathalai* or a *P. cathalai*-like ancestor to the modern *Apodemus*, remained stable regarding to molar shape over a time span of 11 Myr.

Molar size increases along the *Stephanomys* lineage (figure 3*b*). This increase occurs stepwise, with a first, slight increase in size from *P. hispanicus* to *Occitanomys*.

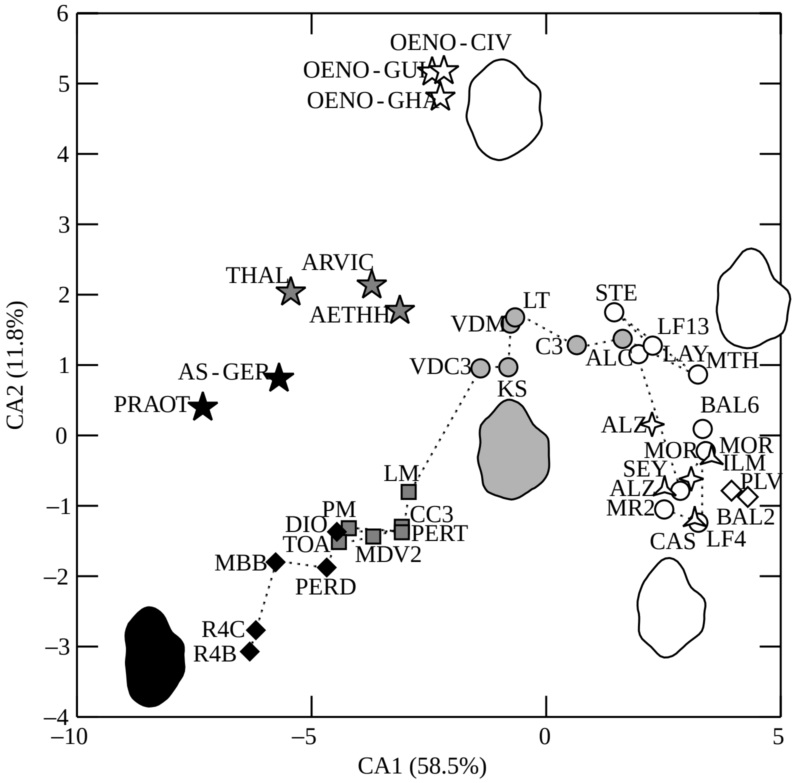

Figure 2. Morphological differentiation of the upper molar along the *Stephanomys* lineage and comparison with modern taxa of known diet. Dots are group means of the different species/deposits on the first canonical plane. The average morphology of some samples is visualized by reconstructed outlines. Symbols for fossil deposits as on figure 1. Modern taxa are shown by stars, black represents omnivorous, grey a trend toward herbivory and open stars herbivorous with an achieved stephanodont dental pattern.

A more important size increase is related to the apparition of the first *Stephanomys*. *Occitanomys* is decreasing in size at this time owing to interspecific competition (Renaud *et al.* 1999). This genus persists thereafter until its extinction during the Late Pliocene (Agustí & Julia 1990; Michaux *et al.* 1997). *Stephanomys* survives *Occitanomys* until the Plio-Pleistocene boundary and during the Late Miocene, experiences a diversification leading to several species of different size, for example, the small *S. minor* and the intermediate *S. calveti*. *S. donnezani* experiences an important intraspecific size increase from the first (MTH, ~3.3 Myr) to the last representative (LAY, ~2.9 Myr). *Stephanomys thaleri* reaches the largest size documented in the *Stephanomys* lineage shortly before its extinction (MR2, ~1.7 Myr). Once again, the lineage related to *Apodemus* did not experience notable changes in size over its evolution.

3. TEMPORAL TRENDS IN RODENT EVOLUTION

The radiation of the murine rodents occurred in a relatively stable, humid and warm environment. During the Late Miocene, the climate changed stepwise (figure 3*c*,*d*) towards drier and more seasonal conditions (An *et al.* 2001). The climate during the Pliocene became generally cooler, drier, and more seasonal (deMenocal 2004). By 3.5 Myr ago, an intensification of the monsoon led to a double seasonality (combination of temperature and precipitation) in the Mediterranean region (Suc *et al.* 1995; An *et al.* 2001). This aridification continued in steps at 2.8, 1.7 and 1.0 Myr ago (deMenocal 2004). Since 2.5 Myr ago, modern vegetation seems to have been established in mid-latitude regions (Dupont & Leroy 1999). The Pleistocene climate is dominated by pronounced glacial–interglacial cycles, expressed by the enhanced variability of $\delta^{18}O$ values of benthic foraminifers (figure 3*c*; Zachos *et al.* 2001). The cold phases were more arid than the warm ones (Dupont & Leroy 1995). The climate change had an important impact on the vegetation leading to a general expansion of open environments, namely grasslands, dominated in many regions by the expanding C4 plants (figure 3*d*; Cerling *et al.* 1993, 1998; Pagani *et al.* 1999; Fox & Koch 2003).

Modern species like *Apodemus*, a member of the Palaearctic fauna, can be found over a large range of latitude, for example, from North Africa to Scandinavia in the western part of its distribution (Wilson and Reeder 1993). It can, therefore, tolerate wide ranges of temperature. Consequently, a direct influence of climate on rodent evolution seems unlikely for such a species, but a climatic influence could be driven by changes in the vegetation. *Apodemus* is today associated with a forest cover (mainly deciduous forest) producing the seeds composing the major part of its diet (Montgomery & Montgomery 1990). Despite the fact that vegetation evolved significantly over the last 12 Myr, the forest habitat persisted throughout (Fauquette *et al.* 1999). The mosaic landscape provided habitat for omnivorous species like *Apodemus*. Hence, selective forces favouring morphological evolution should have been reduced in the *Apodemus*-related lineage. This is expressed by the relative morphological stability of this lineage (figure 3*a*,*b*).

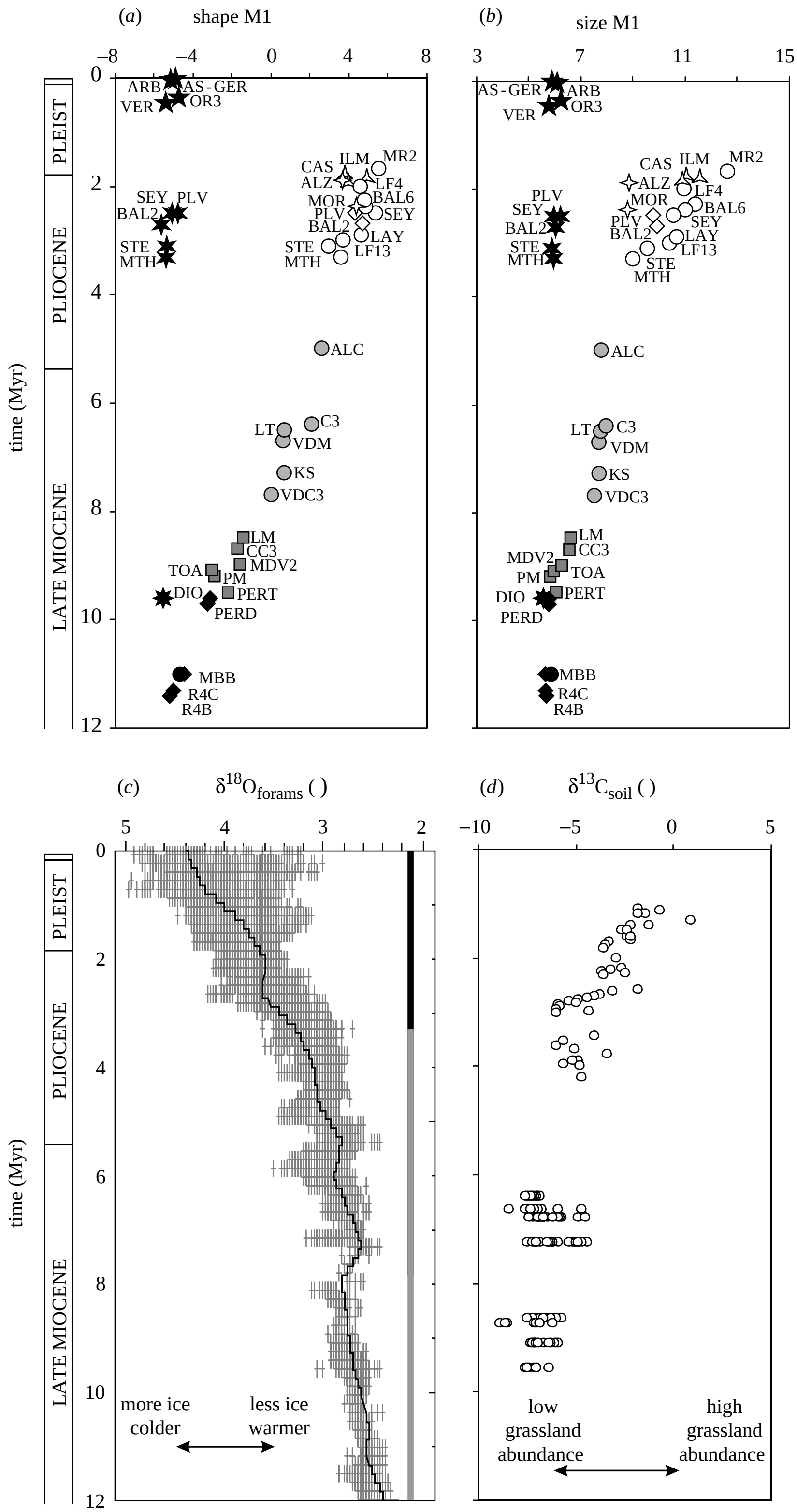

Figure 3. Size and shape evolution compared with the environmental record for the last 12 Myr. (*a*) Shape of the first upper molar, estimated by mean scores on the first canonical axis (69.9% of the among-group variance) of a MANOVA on the Fourier coefficients, based on an outline analysis of molars of the lineages leading to *Stephanomys* on the one hand and to *Apodemus* on the other hand. (*b*) Size of the first upper molar, estimated by A_0. (*c*) Palaeotemperature proxy: global deep-sea oxygen isotope record (after Zachos *et al.* 2001). The grey crosses represent raw data and the full line the general trend (running average). The ice coverage is represented by the vertical bars, in black the Arctic, and in grey the Antarctic. (*d*) Proxy for abundance of C4 grasslands: carbon isotope record of palaeosols (after Fox & Koch 2003).

To further test the possible link between environment and morphological evolution, size and shape values of the upper molar were compared with the marine isotopic record. Because of much more limited precision in dating the continental record compared with the marine one, mammalian data were compared with smoothed $\delta^{18}O$ variations (running average, full line on figure 3*c*). Neither upper molar shape (CA1/$\delta^{18}O$ values $R^2=0.000$, $p=0.993$) nor molar size ($\ln(A_0)/\delta^{18}O$ values $R^2=0.333$, $p=0.063$) were significantly correlated to the palaeotemperature proxy, although the probability for size is close to the threshold value, suggesting an increase in molar size for decreasing temperature. Temperature is known to cause size variations within species of mammals according to Bergmann's rule (Dayan *et al.* 1991). Minor size variations in *Apodemus* could be related to this process (Michaux & Pasquier 1974; Michaux 1983).

Very environmentally tolerant species like *Apodemus* remained stable in molar shape and size over time despite climate changes. Nevertheless, the gradual trend towards drier and colder conditions caused changes in the vegetation cover, which in turn influenced the rodent evolution. The expansion of the grassland opened environmental opportunities. The exploitation of these new resources made specific adaptations necessary because grasses are very abrasive owing to silica in their vegetative parts as well as dust and grit adhering to low-lying plants in open habitats (Janis *et al.* 2002).

The appearance of the highly specialized *Stephanomys* coincides with the onset of the general expansion of grasslands. Contrary to the murine species with an '*Apodemus*-like' dental pattern, *Stephanomys* is characterized by broad molars with swollen cusps and pronounced ridges sliding in corresponding gutters. These characters contribute to an increase in the surface of contact between upper and lower teeth rows and hence the grinding efficiency. An increase in the molar height ameliorates the resistance to wear throughout the life of the animal. All these characters can be interpreted as adaptation to consumption of grasses and an exploitation of newly developed habitats. The further evolution of *Stephanomys* can also be related to different steps of environmental changes. Vegetation in the western Mediterranean area was modified ~3.5 Myr ago because of the establishment of a double seasonality of temperature and precipitation (Suc *et al.* 1995). Large size should allow a better energetic control (Damuth 1993) and may be favoured in more variable and harsh environments. Hence the large size increase observed in *Stephanomys* could be interpreted as a response to the increasing seasonal variability and summer drought. An increasing aridity and a vegetation shift to modern conditions (~2.5 Myr ago) led to the diversification within *Stephanomys*. The environmental influence on the evolution of *Stephanomys* is supported by tight correlation between palaeotemperature and upper molar morphology, including shape (CA1/$\delta^{18}O$ values $R^2=0.686$, $p<0.001$) and size ($\ln(A_0)/\delta^{18}O$ values $R^2=0.759$, $p<0.001$).

Stephanomys did not survive the additional climatic extremes corresponding to the arid glacial and humid interglacial cycles developing at the Plio-Pleistocene boundary. The climatic variability may have been larger than the ecological range of *Stephanomys* and the geographical boundaries of *Stephanomys* in southern France and the Iberian peninsula did not allow the species to escape stress by habitat tracking.

Our results show that there is no predictive pattern of climate-forcing on morphological evolution since climate change had a different impact according to the lineage. The climatic effect is probably not direct, but relayed by the vegetation and dependent on the ecological preferences of the animals. This could explain the different patterns observed in the generalist species *Apodemus* versus the specialist *Stephanomys*. Despite the important environmental change, the habitat of *Apodemus* persisted and this taxon displayed a relative morphological stability over time. In contrast, *Stephanomys* exploited new ecological opportunities provided by the drying climate and expanding grasses in Western Europe since the Late Miocene. The same mechanism has been suggested to drive the evolution of hypsodont mammals during the Neogene in Europe (Jernvall & Fortelius 2002). The increasing specialization would have forced *Stephanomys* to react repeatedly to the ongoing climatic changes. Despite the opening of new ecological opportunities, the climate change apparently did not increase the number of niches available since the diversity of the murine community decreased from the beginning of the Pliocene (Aguilar *et al.* 1999). Owing to the broad climatic variability, an adaptation to a narrow range of conditions would have been unfavourable. In contrast, species able to exploit and sustain a wide range of environmental conditions should have been favoured. This includes a long-term generalist like *Apodemus* and a few specialists adapted to an increasingly common habitat, for example, open habitats and grasslands for *Stephanomys*.

4. CONCLUSIONS

Climate influenced the morphological evolution of *Stephanomys* but this result can not be generalized for all related murine rodents. These climatic influences on *Stephanomys* evolution would not have been direct, but rather indirect through a change in vegetation and hence diet of the rodents. The expansion of grasses, owing to increasing aridity, probably created new ecological opportunities. This would have favoured the evolution of a specialist rodent able to feed on abrasive vegetal matter by a dental adaptation, in that case stephanodonty. The expansion of the ecological resources available is therefore related to the evolution of some specialist species but does not automatically imply an increasing diversity of the community, because increasing environmental variability during the Pliocene may have favoured a broader ecological tolerance. Both a long-term generalist like *Apodemus* and a specialist adapted to abundant resources would have been able to cope with the deteriorating environmental conditions. The same environmental changes can therefore favour opposite patterns of morphological evolution: stability in *Apodemus* and an adaptive increasing specialization in *Stephanomys*.

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REFERENCES

Aguilar, J.-P. & Michaux, J. 1996 The beginning of the age of Muridae (Mammalia: Rodentia) in southern France. *Acta Zool. Cracov.* **39**, 35–45.

Aguilar, J.-P., Michaux, J., Delannoy, J. J. & Guendon, J. L. 1993 A Late Pliocene rodent from Alozaina (Malaga, Spain). *Scr. Geol.* **103**, 1–22.

Aguilar, J.-P., Legendre, S., Michaux, J. & Montuire, S. 1999 Pliocene mammals and climatic reconstruction in the Western Mediterranean area. In *The Pliocene: time of change* (ed. J. H. Wrenn, J.-P. Suc & S. A. G. Leroy), pp. 109–120. Houston, TX, American Association of Stratigraphic Palynologists Foundation.

Aguilar, J.-P., Berggren, W. A., Aubry, M.-P., Kent, D. V., Clauzon, G., Benammi, M. & Michaux, J. 2004 Mid Neogene Mediterranean marine–continental correlations: an alternative interpretation. *Palaeogeogr. Palaeoclimat. Palaeoecol.* **204**, 165–186.

Agustí, J. & Julia, R. 1990 Paleoclimatic inferences from the Plio-Pleistocene continental sequence of the Guadix-Baza Basin (Spain). In *Evolution climatique dans le domaine méditerranéen au Néogène* (ed. J.-P. Suc), vol. XVII, pp. 269–279. Montpellier-Barcelone, Montpellier: Interim-Colloquium du R.C.M.N.S., Colloque associé du C.N.R.S..

Alroy, J., Koch, P. B. & Zachos, J. 2000 Global climate change and North American mammalian evolution. In *Deep time. Paleobiology's perspective* (ed. D. H. Erwin & S. L. Wing) *Paleobiology, Supplement to Volume 26(4)*, pp. 259–288. Lawrence, KS, Allen Press.

An, Z., Kutzbach, J. E., Prell, W. L. & Porter, S. C. 2001 Evolution of Asian monsoons and phased uplift of the Himalaya-Tibetan plateau since Late Miocene times. *Nature* **211**, 62–66.

Bachelet, B. & Castillo Ruiz, C. 1990 Radiation évolutive et lignées chez les *Stephanomys* (Rodentia, Mammalia), muridés dominants du Pliocène d'Europe sud-occidentale. *C. R. Acad. Sci., Sér. II* **311**, 493–499.

Cerling, T. E., Wang, Y. & Quade, J. 1993 Expansion of C_4 ecosystems as an indicator of global ecological change in the Late Miocene. *Nature* **361**, 344–345.

Cerling, T. E., Ehleringer, J. R. & Harris, J. M. 1998 Carbon dioxide starvation, the development of C_4 ecosystems, and mammalian evolution. *Phil. Trans. R. Soc. B* **353**, 159–171.

Cordy, J.-M. 1978 Caractéristiques générales de la micro-évolution du genre *Stephanomys* (Rodentia, Muridae). *Bull. Soc. Géol. France* **XX**, 815–819.

Crusafont Pairo, M. 1965 Observations à un travail de M. Freudenthal et P.Y. Sondaar sur les nouveaux gisements à Hipparion d'Espagne. *Kon. Nederl. Akad. Wet. Proc. (B)* **68**, 121–131.

Damuth, J. 1993 Cope's rule, the island rule and the scaling of mammalian population density. *Nature* **365**, 748–750.

Dayan, T., Simberloff, D., Tchernov, E. & Yom-Tov, Y. 1991 Calibrating the paleothermometer: climate, communities, and the evolution of size. *Paleobiology* **17**, 189–199.

deMenocal, P. B. 2004 African climate and faunal evolution during the Pliocene–Pleistocene. *Earth Planet. Sci. Lett.* **220**, 3–24.

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 Theriol.* **39**, 357–364.

Dieterlen, F. 1967 Ökologische Populationsstudien an Muriden des Kivugebietes (Congo). Teil I. *Zool. Jahrb. Abt. Syst. Ökologie Geogr. Tiere* **94**, 369–426.

Dupont, L. M. & Leroy, S. A. G. 1995 Steps towards drier climatic conditions in northwestern Africa during the upper Pliocene. In *Paleoclimate and evolution with emphasis on human origins* (ed. E. S. Vrba, G. H. Denton, T. C. Partridge & L. H. Burckle), pp. 289–298. New Haven CT, Yale University Press.

Dupont, L. M. & Leroy, S. A. G. 1999 Climatic changes in the Late Pliocene of NW Africa from a pollen record on an astronomically tuned timescale. In *The Pliocene: time of change* (ed. J. H. Wrenn, J.-P. Suc & S. A. G. Leroy), pp. 145–161. Houston, TX, American Association of Stratigraphic Palynologists Foundation.

Fauquette, S., Suc, J.-P., Guiot, J., Diniz, F., Feddi, N., Zheng, Z., Bessais, E. & Drivaliari, A. 1999 Climate and biomes in the West Mediterranean area during the Pliocene. *Palaeogeogr. Palaeoclimat. Palaeoecol.* **152**, 15–36.

Fox, D. L. & Koch, P. L. 2003 Tertiary history of C4 biomass in the Great Plains, USA. *Geology* **31**, 809–812.

Gmelig Meyling, C. & Michaux, J. 1973 Le genre *Stephanomys* Schaub 1938 (Rodentia, Mammalia); son évolution au Pliocène supérieur. *C. R. Acad. Sci. Sér. D* **277**, 1441–1444.

Janis, C. M., Damuth, J. & Theodor, J. M. 2002 The origins and evolution of the North American grassland biome: the story from the hoofed mammals. *Palaeogeogr. Palaeoclimat. Palaeoecol.* **177**, 183–198.

Jernvall, J. & Fortelius, M. 2002 Common mammals drive the evolutionary increase of hypsodonty in the Neogene. *Nature* **417**, 538–540.

Manly, B. F. J. 1994. Multivariate statistical methods. A primer, 2nd edn. London: Chapman & Hall/CRC.

Martín-Suárez, E. & Mein, P. 1998 Revision of the genera *Parapodemus*, *Apodemus*, *Rhagamys* and *Rhagapodemus* (Rodentia, Mammalia). *Geobios* **31**, 87–97.

Michaux, J. 1977 Les muridés actuels et fossiles. In *Aspects modernes des recherches sur l'évolution* (ed. J. Bons), vol. 4, pp. 133–143. Montpellier, École Pratique des Hautes Études.

Michaux, J. 1983 Aspects de l'évolution des Murinés (Rodentia, Mammalia) en Europe sud-occidentale. *Colloque International du CNRS, n°330, Modalités et Rythmes de l'Évolution Biologique*, pp. 195–199. France, Dijon.

Michaux, J. & Pasquier, L. 1974 Dynamique des populations de mulots (Rodentia, *Apodemus*) en Europe durant le Quaternaire. Premières données. *Bull. Soc. Géol. France* **XVI**, 431–439.

Michaux, J., Aguilar, J.-P., Montuire, S., Wolff, A. & Legendre, S. 1997 Les Murinae (Rodentia, Mammalia) néogènes du Sud de la France: évolution et paléoenvironnements. *Geobios. Mém. Spéc.* **20**, 379–385.

Montgomery, S. S. J. & Montgomery, W. I. 1990 Intrapopulation variation in the diet of the wood mouse *Apodemus sylvaticus*. *J. Zool. Lond.* **222**, 641–651.

Pagani, M., Freeman, K. H. & Arthur, M. A. 1999 Late Miocene atmospheric CO_2 concentrations and expansion of C_4 grasses. *Science* **285**, 876–879.

Renaud, S. & Michaux, J. R. 2003 Adaptive latitudinal trends in the mandible shape of *Apodemus* wood mice. *J. Biogeogr.* **30**, 1617–1628.

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). *Palaeogeogr. Palaeoclimat. Palaeoecol.* **184**, 161–173.

Renaud, S., Michaux, J., Jaeger, J.-J. & Auffray, J.-C. 1996 Fourier analysis applied to *Stephanomys* (Rodentia, Muridae) molars: nonprogressive evolutionary pattern in a gradual lineage. *Paleobiology* **22**, 255–265.

Renaud, S., Michaux, J., Mein, P., Aguilar, J.-P. & Auffray, J.-C. 1999 Patterns of size and shape differentiation during the evolutionary radiation of the European Miocene murine rodents. *Lethaia* **32**, 61–71.

Reumer, J. W. F. 1995 The effect of paleoclimate on the evolution of the Soricidae (Mammalia, Insectivora). In *Paleoclimate and evolution with emphasis on human origins* (ed. E. Vrba, G. Denton, T. Partridge & L. Burckle), pp. 135–137. New Haven, CT and London, Yale University Press.

Schaub, S. 1938 Tertiäre und Quartäre Murinae. *Abh. Schweiz. Paleontol. Ges. Basel* **61**, 1–39.

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

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 Zool. Cracov.* **38**, 3–16.

Thenius, E. 1951 Die jungtertiäre Säugetierfauna des Wiener Beckens in ihrer Beziehung zu Stratigraphie und Ökologie. *Erdölzeitung* **5**, 52–54.

Tobien, H. 1967 Subdivision of pontian mammalian faunas. Committee Mediterranean Neogene Stratigraphy, Proc. IV Session, Bologna. *G. Geol. 2* **XXXV**, 1–5.

van Dam, J. 1996 Stephanodonty in fossil murids. In *Advances in morphometrics* (ed. L. F. Marcus, M. Corti, A. Loy, G. J. P. Naylor & D. E. Slice), vol. 84, pp. 449–461. New York, Plenum Press.

van Dam, J. A. 1997 The small mammals from the upper Miocene of the Teruel-Alfambra region (Spain): paleobiology and paleoclimatic reconstructions. *Geol. Ultraiect.* **156**, 1–204.

van de Weerd, A. 1976 Rodent faunas of the Mio-Pliocene continental deposits of the Teruel-Alfambra region, Spain. *Utrecht Micropaleontol. Bull. Spec. Publ.* **2**, 1–216.

van der Meulen, A. J. & Daams, R. 1992 Evolution of Early-Middle Miocene rodent faunas in relation to long-term palaeoenvironmental changes. *Palaeogeogr. Palaeoclimat. Palaeoecol.* **93**, 227–253.

Van Valen, L. 1973 Body size and numbers of plants and animals. *Evolution* **27**, 27–35.

Wilson, D. E. & Reeder, D. M. 1993. Mammals species of the world. A taxonomic and geographic reference. Washington: Smithonian Institution Press.

Zachos, J., Pagani, M., Sloan, L., Thomas, E. & Billups, K. 2001 Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science* **292**, 686–693.

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