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Influence of biotic and abiotic environment on dental size and shape evolution in a Late Miocene lineage of murine rodents (Teruel Basin, Spain)

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Abstract

Dental size and shape evolution in a Late Miocene lineage of murine rodents is analyzed, based on a set of deposits from the Teruel Basin (Spain). The lineage leads from *Progonomys hispanicus*, characterized by small and primitive molars, to *Stephanomys ramblensis*, characterized by large and specialized, stephanodont molars. A dietary change from granivory to herbivory is assumed to accompany this morphological change. Fourier analysis of molar outlines shows that size and shape evolve gradually with time. However, evolutionary rates of size and shape of upper and lower molars differ along the lineage. This suggests that mosaic evolution occurs with respect to upper and lower molars, and that size and shape are under different selective pressures. Comparison with biotic factors, i.e. diversity of the local community, and abiotic parameters, i.e. climatic reconstruction based on the rodent community and marine $\delta^{18}\text{O}$ record, suggests that morphological evolution may be influenced by environmental variations. Climatic changes are suggested to influence biotic variations via opening of new ecological niches, favoring morphological evolution in murine rodents during the Late Miocene. © 2002 Elsevier Science B.V. All rights reserved.

Keywords: Fourier analysis; evolutionary trends; morphology

1. Introduction

Environmental changes act on faunas at different scales. First, they influence the composition and dynamics of faunal communities, as exemplified by phases of faunal turn-over associated with climatic fluctuations (Vrba, 1995). Environmental changes also influence the direction and rate of

evolution within a single species or lineage. Gradual evolutionary patterns have been suggested to be associated with stable environmental conditions allowing the progressive evolution of specialized species, while unstable conditions would be associated with stasis by favoring the maintenance of generalist species (Sheldon, 1993, 1996). Alternatively, morphological evolution can be driven by biotic factors such as interspecific competition (Dayan et al., 1990; Dayan and Simberloff, 1994), with niche partitioning, associated with dietary and behavioral divergence, being progressively achieved.

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The present study attempts to quantify the morphological evolution along a Late Miocene lineage of murine rodents, and its relationship with environmental variations. The evolution along this lineage is studied using isolated molars from a series of mammal-bearing localities in the Teruel Basin, Spain (Fig. 1). The sequence is dated using magnetostratigraphy (Krijgsman et al., 1996; Garcés et al., 1999), litho- and biostratigraphy (van Dam, 1997; van Dam et al., 2001). The resulting chronological framework allows both reliable estimates of evolutionary rates and comparison with marine climatic records. Size and shape of first upper and lower molars are quantified using an outline analysis based on Fourier transform, and the resulting evolutionary patterns are compared. In order to examine the possible factors influencing morphological evolution, the morphometric results are compared to a range of biotic and abiotic parameters: (1) the diversity of the community, considered as an indicator of interspecific competition; (2) local climatic proxies derived from the rodent community; (3) marine stable isotope proxies from DSDP Site 608 off Spain, providing paleoenvironmental information completely independent from the ro-

dent community, thus avoiding the risk of circular reasoning.

1.1. The studied lineage

The evolutionary lineage considered in this study starts with *Progonomys hispanicus* (~10–8.7 Ma), which evolves into *Occitanomys sondaari* (8.7–7.5 Ma). The next species, *O. adroveri*, experiences a cladogenesis around 7 Ma leading to *O. alcalai* and *Stephanomys ramblensis* (van de Weerd, 1976; van Dam, 1997). Especially the sequence leading to *S. ramblensis* has been considered as a valuable example of phyletic gradualism on the basis of progressive size increase and change in the dental pattern (Cordy, 1976, 1978; van de Weerd, 1976; van Dam, 1996, 1997). The evolution along this lineage leads from small and primitive molars in *P. hispanicus* to large and highly specialized molars in *Stephanomys* with *Occitanomys* having intermediate features (Fig. 2). The dental morphology of *Stephanomys* and to a lesser extent *Occitanomys* typifies a specialization named ‘stephanodonty’, which is characterized by the development of longitudinal crests joining the cusps in a garland-like dental pattern on the upper molars (Schaub, 1938; Misonne, 1969). It has been interpreted as an adaptation to grass-eating by analogy with the extant African stephanodont murines *Oenomys* (Dieterlein, 1967) and *Aethomys* (Denys, 1994), and on the basis of functional morphological arguments (Michaux, 1978; van Dam, 1996). Compared to *Occitanomys* and *Stephanomys*, *Progonomys* has a primitive murine dental pattern, which can be associated with an omnivorous–granivorous diet.

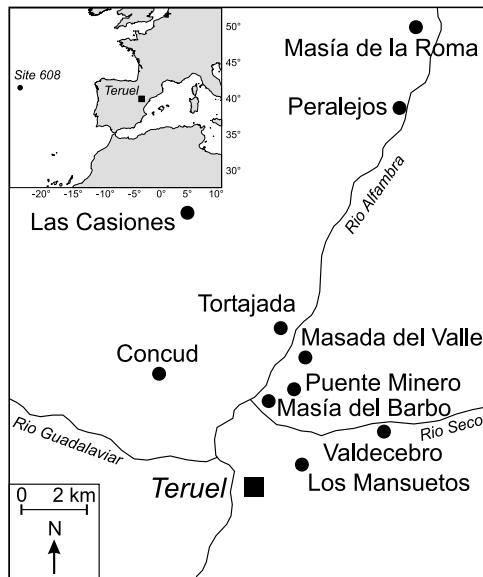


Fig. 1. Location of the mammal-bearing deposits considered in this study (Teruel Basin, Spain) and of the DSDP Site 608.

2. Material and methods

2.1. Geological and chronological setting

The material used in this study comes from 11 mammal-bearing localities located in the Teruel Basin, Spain (Fig. 1). The Teruel Basin is a NNE–SSW striking basin approximately 100 km long and 15 km wide. It is filled with a fairly complete Middle to Upper Neogene alluvial and

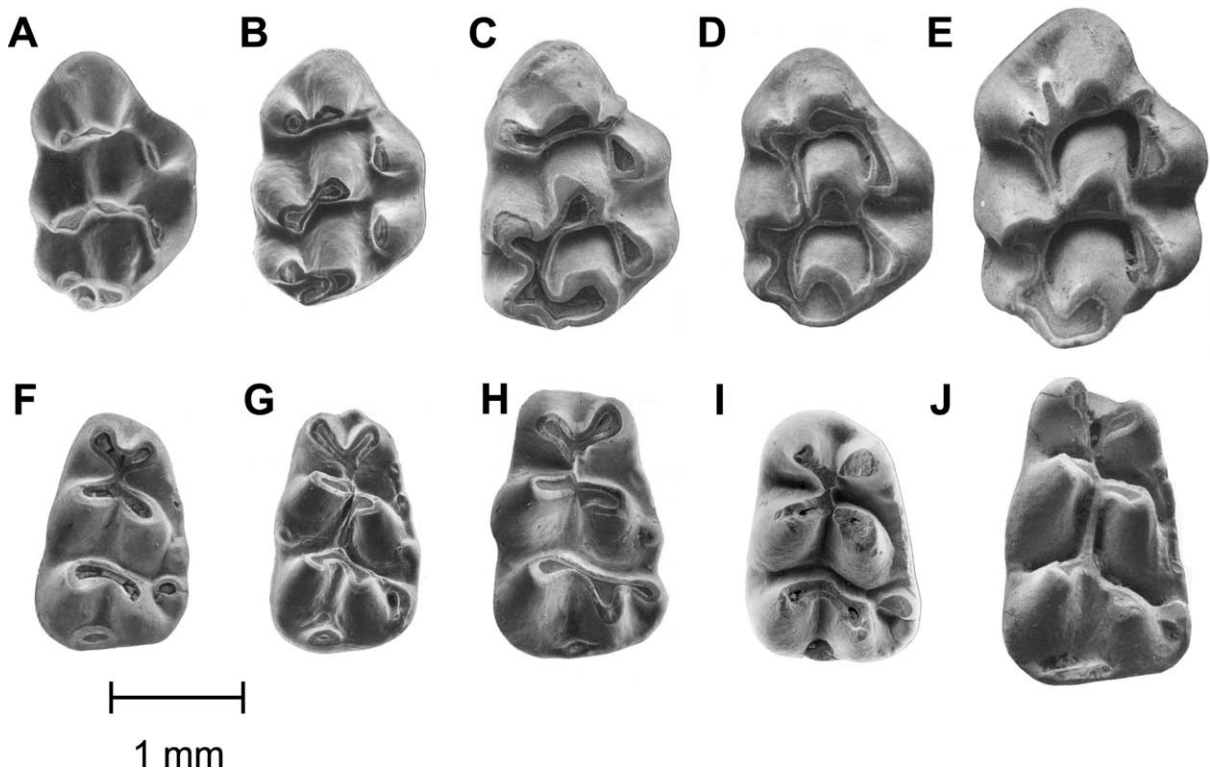


Fig. 2. Right molars exemplifying the morphological changes along the lineage, from the most primitive to the most derived, stephanodont, dental pattern. Upper molars: (A) *Progonomys hispanicus*; (B) *Occitanomys sondaari*; (C) *Occitanomys adroveri*; (D) *Occitanomys alcalai*; (E) *Stephanomys ramblensis*. Lower molars: (F) *P. hispanicus*; (G) *O. sondaari*; (H) *O. adroveri*; (I) *O. alcalai*; (J) *S. ramblensis*.

lacustrine succession exceeding 500 m in thickness (Moissenet, 1989). Most fossil mammal remains are found in organic-rich marlstones and claystones, or lignites associated with carbonate lithofacies (van Dam, 1997; van Dam et al., 2001).

The selected mammal-bearing localities are given in Table 1. They exemplify the successive associations characterizing the local biozones J–M, which can be correlated to Mammal Neogene units 10–13 (Mein, 1990). Ages for the successions were established by linear interpolations based on magneto-, litho- and biostratigraphy and evolutionary stages in murines (van Dam, 1997; van Dam et al., 2001) and calibrated according to the time scale of Cande and Kent (1995).

2.2. Material

We analyzed 220 first upper molars and 167

first lower molars from the 11 localities (Table 1). Only one species of the *Progonomys hispanicus*–*Occitanomys*–*Stephanomys* lineage is present at each locality, except in the two most recent deposits, VDC3 and KS. The material belongs to the collections of Utrecht University and the National Museum of Natural History, Madrid.

2.3. Fourier analysis of molar outlines

In geometric morphometrics landmark and outline analysis are used to describe the morphology of biological objects (e.g. Rohlf and Bookstein, 1990). Previously, the morphological changes along the *Progonomys hispanicus*–*Occitanomys*–*Stephanomys* lineage have been evaluated using the first of these methods, showing a trend towards broadening of the molars, straightening of the posterior border, and alignment of valleys

Table 1

Age and sample size of the first upper molars (M1/) and first lower molars (M/1) within the deposits (Teruel Basin, Spain)

Code	Locality	Age	Local zone	MN units	Genus	Species	M1/	M/1
KS	Las Casiones	6.1	M2	13	<i>Stephanomys</i>	<i>ramblensis</i>	20	15
					<i>Occitanomys</i>	<i>alcalai</i>	18	15
VDC3	Valdecebro 3	6.3	M1	13	<i>Stephanomys</i>	<i>ramblensis</i>	21	18
					<i>Occitanomys</i>	<i>alcalai</i>	14	10
CC3	Concud 3	6.9	L	12	<i>Occitanomys</i>	<i>adroveri</i>	20	14
LM	Los Mansuetos	6.9	L	12	<i>Occitanomys</i>	<i>adroveri</i>	19	15
MDV2	Masada del Valle 2	7.3	L	12	<i>Occitanomys</i>	<i>adroveri</i>	20	15
TOA	Tortajada A	8.1	K	11	<i>Occitanomys</i>	<i>sondaari</i>	20	15
PM	Puente Minero	8.3	K	11	<i>Occitanomys</i>	<i>sondaari</i>	20	15
PERD	Peralejos D	8.7	J3	10	<i>Progonomys</i>	<i>hispanicus</i>	16	9
MBB	Masia del Barbo 2B	9.2	J2	10	<i>Progonomys</i>	<i>hispanicus</i>	20	15
ROM4C	Masia de la Roma 4C	9.5	J1	10	<i>Progonomys</i>	<i>hispanicus</i>	8	9
ROM4B	Masia de la Roma 4B	9.6	J1	10	<i>Progonomys</i>	<i>hispanicus</i>	4	2

Local zones, Mammal Neogene (MN) units and interpolated numerical age (Ma) after van Dam, 1997 and van Dam et al., 2001.

landmarks, associated with increasing stephanodonty (van Dam, 1996). That study was based on 19 two-dimensional landmarks defined on the first upper molar along the outline and in occlusal valleys. This method allows visualization of shape differences by grid deformations (Bookstein, 1991), and information from the central (non-outline) parts of the tooth is used as well. A disadvantage is that on teeth the landmarks are mostly points of maximum curvature along the outline, more sensitive to some error in their location than points defined as intersection of structures.

The description can also be focused on the outline and analyze this feature in detail using Fourier analysis. This approach has been applied successfully to analyze geographic and evolutionary differentiation in rodents (Renaud, 1999; Renaud et al., 1999a,b) and has been chosen here to analyze the morphological differentiation along the *Progonomys*–*Occitanomys*–*Stephanomys* lineage.

The outline corresponds to the two-dimensional projection of the tooth viewed from the occlusal surface. For each tooth, the x and y coordinates of 64 points equally spaced along the outline were extracted semi-automatically using an optical image analyzer. The starting point of the outline was defined at the maximum of curvature on the anterior part of the tooth. From these coordinates, 64 radii, corresponding to the distance of each point to the center of gravity of the tooth, 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 decreasing wavelength (harmonics) according to the formula:

$$r(s) = a_0 + \sum_K^{n=1} [a_n \cos (s/L2\pi n) + b_n \sin (s/L2\pi n)]$$

where r is the radius at the abscissa s along the outline, L the perimeter, K the number of points along the outline, and n the rank of the harmonic. The outline is therefore described by the set of Fourier coefficients a_n and b_n .

To obtain coefficients dependent only on shape, the size is standardized by dividing all the Fourier coefficients by the zeroth harmonic, a_0 , which is proportional to the diameter of the best-fit circle to the digitized outline and is considered as a reliable size estimator (Ehrlich and Weinberg, 1970). A reconstruction of the outline corresponding to any set of Fourier coefficients can be obtained using the inverse Fourier transform, following processes inverse to those used to calculate the Fourier coefficients (Rohlf and Archie, 1984).

A characteristic of the 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 on related species (Renaud et al., 1999b) indicated that the effect of the measurement error can be limited by considering only Fourier coefficients up to the ninth harmonic for the upper molar and up to the sixth for the lower molars.

2.4. *Multivariate analysis of variance (MANOVA) on the Fourier coefficients*

A set of 18 Fourier coefficients (i.e. nine harmonics) for each upper molar and of twelve coefficients (i.e. six harmonics) for each lower molar is obtained. A MANOVA was performed on these variables in order to evaluate the importance of the among-group differentiation relatively to within-group variation. In our analysis, the groups correspond to the different fossil species within the different deposits. Associated with the MANOVA, canonical discriminant functions are estimated, which are usually sufficient to account for almost all of the important group differences (Manly, 1994). The scores of the group means can be plotted on these canonical axes to visualize the patterns of morphological differentiation. A test of significance for among-groups differences (Wilk's Lambda test) is also provided (Marcus, 1993).

3. Results

3.1. *Patterns of morphological differentiation*

A shape differentiation among the different samples exists for the upper molars (Wilk's Lambda = 0.024, degree of freedom (df)₁ = 216, df ₂ = 1935, $P < 0.001$) as well as for the lower molars (Wilk's Lambda = 0.061, df ₁ = 144, df ₂ = 1242, $P < 0.001$). For both upper and lower molars, the first two canonical axes account for most of the among-group variance, and the following canonical axes are of minor importance (below 10% of the among-group variance) and are therefore not considered here.

For the upper molars (Fig. 3A), the shape differentiation corresponds mainly to a distribution of the groups along the first canonical axis (70.6%

of the among-group variance), approximately according to their species determination and age. Samples from a same species are clustered together. The only exception is *Progonomys hispanicus*, displaying a large intraspecific variance and whose youngest representative (PERD) is closest to *Occitanomys sondaari* than to the other samples of *P. hispanicus*. At one side of the first canonical axis (CA1) are located the oldest samples, corresponding to *P. hispanicus*. Opposed to *P. hispanicus* along CA1 are the samples corresponding to *Stephanomys ramblensis*. Between these extremes, the different species of *Occitanomys* are segregated according to their age: first *O. sondaari*, then *O. adroveri* and finally *O. alcalai*. The second axis (CA2) accounts for only a limited part of the group differentiation (14.4% of the among-group variance) and is more difficult to interpret. It shows a morphological trend leading from the oldest *P. hispanicus* (ROM4B and ROM4C) to *O. adroveri*, subsequently reversed from *O. adroveri* to *O. alcalai* and finally *S. ramblensis*.

The reconstruction of the outlines corresponding to some group means allows to visualize shape changes associated with this morphological differentiation. The trend from *Progonomys hispanicus* towards *Stephanomys ramblensis* is characterized by a progressive broadening of the upper molars, in agreement with previous analyses (van Dam, 1996). The differences associated with the trend along CA2 are small but involve more a prominent anterior part and tubercles for *P. hispanicus* and *S. ramblensis*.

The results based on the lower molars (Fig. 3B) are similar to those based on the upper molars. A differentiation exists along CA1 (57.4% of the among-group variance) corresponding to the age of the samples. The main difference with upper molars results is that CA2 (14.5% of the among-group variance) corresponds to a divergence between the two most recent species *Occitanomys alcalai* and *Stephanomys ramblensis*, as well as a variability among *Progonomys hispanicus* and *Occitanomys sondaari*. However, the group differentiation based on the lower molars is weaker than for the upper molars, with more overlap between the different species. This is a general feature for this kind of rodents (Renaud, 1999; Renaud et

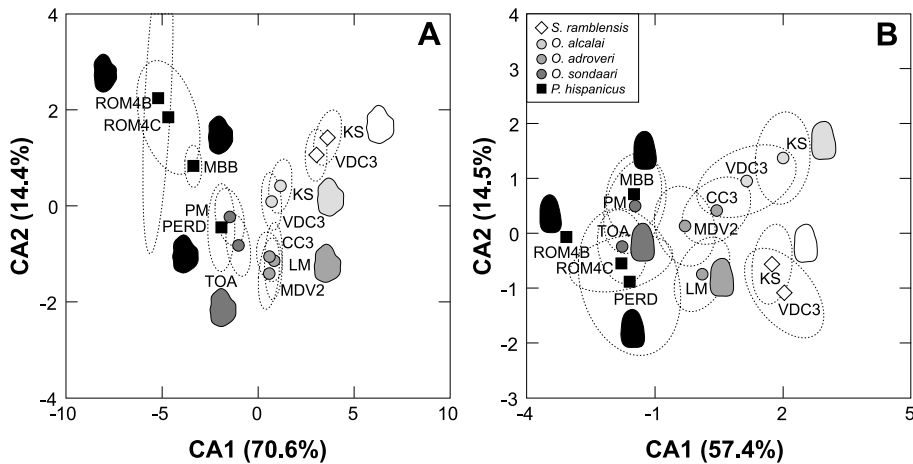


Fig. 3. Morphological differentiation. (A) Upper molars; (B) lower molars. Group means, 95% confidence ellipse and reconstructed outlines are represented on the first two canonical axes. The labels correspond to the locality code (Table 1).

al., 1999a) because the lower molar outlines display less characteristic features than the upper molar ones. Reconstructed outlines of some group means nevertheless allow to visualize the shape changes along the lineage. Lower molars are broadening from the oldest to the youngest groups along CA1. Variations along CA2 correspond to more prominent tubercles for *S. ramblensis* compared to *O. alcalai*.

3.2. Relationship between size and shape of the upper and lower molars

The *Progonomys–Stephanomys* lineage has been recognized as an example of phyletic evolution in both shape and size (van de Weerd, 1976; van Dam, 1996, 1997). Therefore it is important here

to quantitatively estimate size evolution in the context of the outline analysis, and to compare the resulting patterns with shape evolution. The zeroth harmonic a_0 was selected to represent size, and the scores on CA1, accounting for most of the group differences for both the upper and lower molars, were used to quantify shape. The relations between size and shape are comparable for the upper and the lower molars (Table 2; Figs. 4A,B). However, discrepancies exist between size and shape, partly due to the cladogenesis between *Occitanomys alcalai* and *Stephanomys ramblensis* in the youngest samples. The upper molars increase in size after *Occitanomys sondaari*, while shape changes mainly occur earlier (Fig. 4A). This results in a non-linear relationship between size and shape. The lower molars exhibit corre-

Table 2
Correlation of size (a_0), shape (estimated by CA1) and time for the whole lineage (Total) and for each branch separately (*P.–O.*: *Progonomys–Occitanomys*; *P.–S.*: *Progonomys–Stephanomys*)

			Total		<i>P.–O.</i>		<i>P.–S.</i>	
			r^2	<i>P</i>	r^2	<i>P</i>	r^2	<i>P</i>
M1/	CA1	size	0.763	0.000	0.745	0.001	0.833	0.000
	CA1	time	0.911	0.000	0.919	0.000	0.970	0.000
	size	time	0.604	0.002	0.732	0.001	0.831	0.000
M/1	CA1	size	0.600	0.002	0.447	0.024	0.909	0.000
	CA1	time	0.896	0.000	0.878	0.000	0.872	0.000
	size	time	0.595	0.002	0.619	0.004	0.875	0.000

First upper molars (M1/) and first lower molars (M/1).

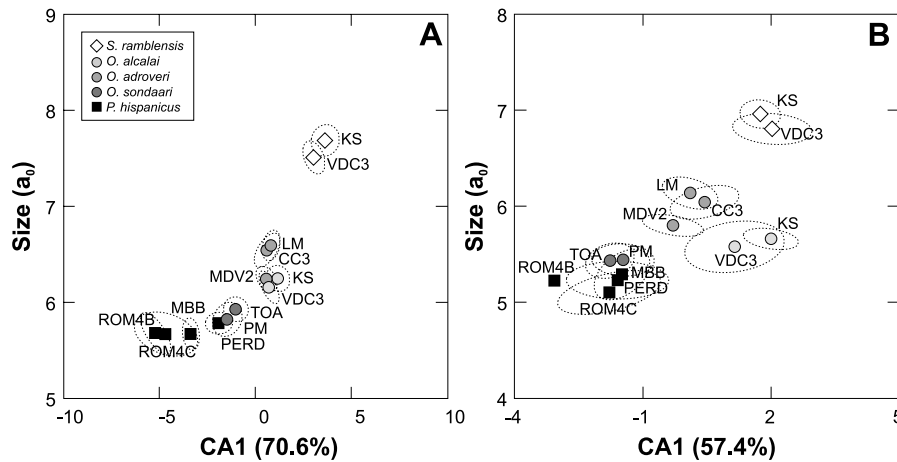


Fig. 4. Size and shape relationship. (A) Upper molars; (B) lower molars. Group means and 95% confidence ellipse are plotted in a morphological space defined by size and shape.

lated evolution in size and shape from *Progonomys hispanicus* to *S. ramblensis*, but *O. alcalai* strongly departs from this general relationship (Fig. 4B). The correlation between size and shape is therefore much stronger if only the *Progonomys*–*Stephanomys* branch of the lineage is considered (Table 2).

Size evolution of the upper and lower molars is highly correlated ($r^2 = 0.984$, $P < 0.001$), and therefore only graphs with upper molar size will be displayed hereafter. Shape evolution, estimated by scores on CA1, is also highly correlated between upper and lower molars ($r^2 = 0.823$, $P < 0.001$). However, small deviations from the general relationship exist. The evolution from the *Progonomys hispanicus* from ROM4C to *Occitanomys sondaari* involves an evolution of the upper molar, while the lower molar remains sta-

ble. On the contrary, the evolution from *O. adroveri* to *O. alcalai* mainly involves changes of the lower molars.

3.3. Morphological evolution and environmental variations

The biodiversity of both the murine and the rodent community has been estimated by species richness, adjusted by rarefaction to compensate difference in sample size (after van Dam, 1997; van Dam et al., 2001). This approach provides species richness values adjusted to the sample size (i.e. number of first and second molars) of the deposit with the lowest abundance. In our set of localities, the smallest sample sizes correspond to the stratigraphically very close localities ROM4B and ROM4C. The frequencies observed

Table 3

Probability of correlation of size and shape evolution with environmental parameters: adjusted species richness of the murine and rodent community (van Dam, 1997); humidity/temperature and predictability/seasonality type (van Dam and Weltje, 1999); benthic foraminifer isotopic data from NE Atlantic (Wright et al., 1991)

		Murine Sr	Rodent Sr	Humidity/temp.	Predict./season. type	$\delta^{18}\text{O}$
M1/	a_0	0.029	0.674	0.116	0.060	0.011
	CA1	0.000	0.430	0.021	0.002	0.002
M/1	a_0	0.024	0.638	0.116	0.051	0.017
	CA1	0.003	0.497	0.068	0.032	0.000

Significant probabilities are in bold. First upper molars (M1/) and first lower molars (M/1).

in these two deposits were added and subsampling of the other localities was based on these totals. Adjusted murine species richness values are never very high in the deposits considered here, varying between one species in the oldest deposits to values around three species in the youngest localities. However, this parameter is highly correlated with the morphological characters, especially shape of the upper and lower molars. On the contrary, morphological evolution is independent of the adjusted rodent species richness (Table 3).

Abiotic environmental variations have been estimated using several parameters. Indications on the local conditions were provided by the variations in relative abundances of ecological groups within the rodent community as a whole (van Dam and Weltje, 1999). Humidity was found to be correlated with temperature, and predictability of the climate (in this case defined as between-year variation) was found to correlate with seasonality type. The climate appears to have fluctuated between more wet, cool, cool–warm seasonal, and predictable conditions on the one hand, and more arid, warm, wet–dry seasonal and unpredictable conditions on the other hand. On the whole these climatic parameters are weakly correlated with morphological evolution (Table 3).

Morphological evolution was also compared to benthic foraminifer stable isotopic data from DSDP Site 608 in the NE Atlantic (Fig. 2). We used values of $\delta^{18}\text{O}$ (Wright et al., 1991), with an age model recalibrated according to the time scale of Cande and Kent (1995). Oscillations of $\delta^{18}\text{O}$ have been interpreted as glacial–interglacial cycles with intervals of increasing ice volume between 10–8.5 and 7.5–6.5 Ma (Wright et al., 1991). The $\delta^{18}\text{O}$ record displays good correlations with

the morphological evolution of all characters (Table 3).

Significant correlations of different environmental proxies with morphological variations could be partly due to an intercorrelation of these variables (Table 4). It appears that murine species richness is well correlated to the various abiotic parameters. Additionally humidity and seasonality type are linked together; other data do not display significant relation.

4. Discussion

Our morphometric analysis corroborates previous interpretations for the *Progonomys–Occitanomys–Stephanomys* lineage. Taxonomic identifications of species are strongly supported by clustering of samples belonging to the same species in the morphological space, especially for the upper molars (Fig. 3). The lineage had been previously recognized as an example of phyletic evolution based on gradual size increase and morphological change (van de Weerd, 1976; van Dam, 1996, 1997), and our results are in agreement with the conclusions of these studies. However, the characters considered here provide a slightly different picture of the evolution along the lineage (Figs. 5A–C).

4.1. Mosaic evolution of the different characters

A general trend of size increase (with the exception of the size decrease of *Occitanomys alcalai*) occurs along the lineage, together with a broadening of the upper and lower molars. However, evolutionary rates are not the same for every

Table 4
Intercorrelation of environmental variables

	Murine Sr	Rodent Sr	Humidity/temp.	Predict./season. type	$\delta^{18}\text{O}$
Murine Sr	–				
Rodent Sr	0.108	–			
Humidity/temp.	0.044	0.629	–		
Predict./season. type	0.002	0.445	0.001	–	
$\delta^{18}\text{O}$	0.068	0.843	0.173	0.238	–

Significant probabilities are in bold.

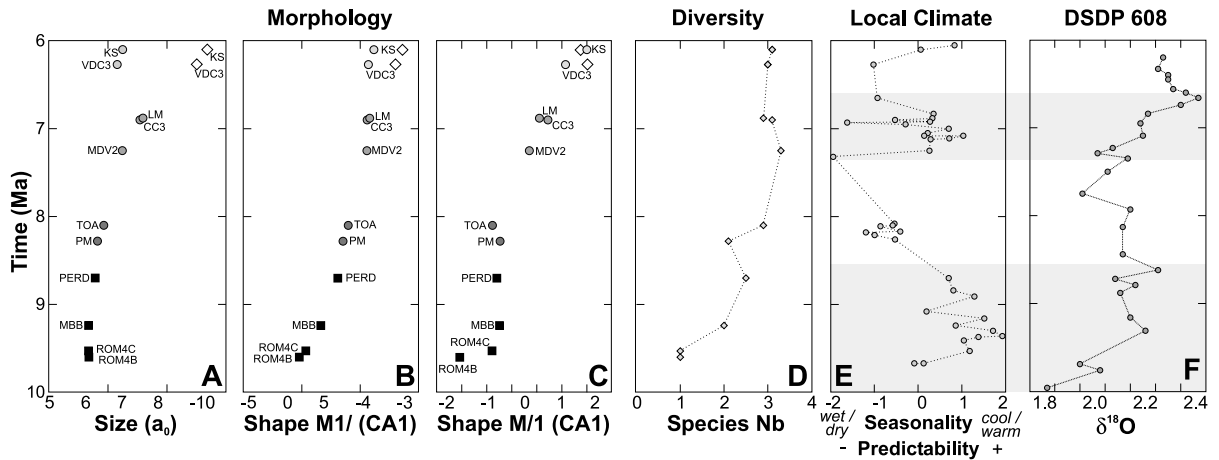


Fig. 5. Comparison of morphological evolution and environmental parameters. (A) Mean size of the upper molars; (B) shape of the upper molars; (C) shape of the lower molars; (D) murine species richness; (E) predictability/seasonality type variations (after van Dam and Weltje, 1999); (F) $\delta^{18}\text{O}$ data from benthic foraminifers of the DSDP Site 608, NE Atlantic (after Wright et al., 1991). In gray, periods of decreasing ice volume.

character. The rate of size evolution is especially high between *Occitanomys adroveri* and its two descendents *O. alcalai* and *Stephanomys ramblensis*. Major shape changes occur earlier along the lineage; for the upper molars within *Progonomys hispanicus*, and for the lower molars between the *O. sondaari* and *O. adroveri* stages.

The studied lineage is therefore characterized by mosaic evolution, with different evolutionary rates in the various characters. This result underlines that variations in size and shape evolution can not be considered to be the expression of a simple allometric relationship. The observed decoupling suggests that the evolution of the various characters result from different ranges of genetic constraints and selective pressures (Renaud et al., 1996). This result is surprising, given that the upper and lower molars work together during chewing, suggesting common functional constraints.

4.2. Influence of interspecific competition on size and shape evolution

Interspecific competition is an important factor structuring ecological communities (Hutchinson, 1959), leading to a partition of the exploitation of the environment between species (Schoener, 1974). Such a partition of ecological niches can

be achieved through size differentiation. Body size in rodents is an important ecological factor since it is linked to the size of the food, and to utilization of microhabitats. If size differences between species are related to avoidance of interspecific competition, a constant size ratio between related species is to be expected: ratios should range from 1.1 and 1.4 with a mean value of 1.28 (Hutchinson, 1959). Such an effect is likely to exist in our two youngest localities, VDC3 and KS, where two morphologically close species from our lineage occur in sympatry. Molar size is closely related to body size in mammals (Legendre, 1989), and *Stephanomys ramblensis* and *Occitanomys alcalai* are characterized by a molar-size ratio of 1.22 (VDC3) and 1.23 (KS), values close to the expected size ratio in the case of interspecific competition avoidance through size differentiation. This result suggests that the acceleration of size evolution between *Occitanomys adroveri* and its two descendent species is related to ecological interactions between the two newly evolved species.

Shape differentiation plays a role in niche partitioning as well. In rodents, different dental morphologies may represent adaptations to different diets, and therefore may be relevant to the avoidance of interspecific competition (Parra et al., 1999; Renaud et al., 1999b). However, this effect

should be limited within our lineage: the sympatric species *Occitanomys alcalai* and *Stephanomys ramblensis* share the broadening trend in the molars, which could be associated with the development of a more herbivorous diet (van Dam, 1997). On the other hand, this morphological trend can play a role in the avoidance of competition with the other members of the community. The amount of interspecific competition has been estimated by the species richness at the level of the murine and rodent community. Variations in murine species richness are highly correlated with morphological evolution (Fig. 5D), in contrast to variations in rodent species richness. This discrepancy could be due to the fact that murine species such as *Occitanomys*, *Stephanomys*, *Parapodemus*, *Apodemus* and *Huerzelerimys* share inherited ecological characteristics leading to a high level of interspecific competition. The divergence of these species was recent at the time considered in our study, since it occurred during the progressive diversification of the murines between 11 and 8.5 Ma, that has been proven to be associated with a partitioning of the community through both size and shape differentiation (Renaud et al., 1999b). Therefore, our results suggest that biotic interactions could influence morphological evolution. However, this effect could be limited by the overall low murine species richness in Europe, compared to Africa and Asia where the murine diversification has been much more successful (Misonne, 1969).

4.3. Role of abiotic environmental factors

Two types of abiotic factors have been compared to the morphological evolution along the *Progonomys–Occitanomys–Stephanomys* lineage (Table 3). Environmental parameters derived from the structure of the rodent community (van Dam and Weltje, 1999) show only a weak correlation with morphological evolution, a surprising result since both records are based on rodents. In contrast, the comparison with the marine $\delta^{18}\text{O}$ record shows a good correlation with morphological evolution (Fig. 5F), mainly due to the general trend towards higher $\delta^{18}\text{O}$ which correlates well with the morphological trend asso-

ciated with the development of the stephanodonty.

The molar shape in our lineage changes in a monotonous way, as does size with the exception of *Occitanomys alcalai*, whereas the climatic parameters show oscillations superimposed to the general trend. These climatic oscillations, apparent in the $\delta^{18}\text{O}$ record (Fig. 5F), are even better expressed in the predictability/seasonality type record (Fig. 5E), or other marine climate-related record (Poore, 1981; Sierro et al., 1993). This discrepancy suggests that short-term environmental variations do not influence morphological evolution, which rather covaries with the long-term climatic trend, displayed by the marine isotopic record.

A case for how climatic shift triggered a phase of accelerated morphological evolution is the response of North African rodents to the environmental variations characterizing the Pliocene–Pleistocene boundary (Renaud et al., 1999a). The climatic shift at the Pliocene–Pleistocene boundary was very important compared to the Late Miocene variations experienced by our lineage. Comparing the amplitude of the $\delta^{18}\text{O}$ variations between the two periods suggest that the climatic change was four-fold more important at the Pliocene–Pleistocene boundary. This suggests that environmental changes during the Late Miocene evolution of the *Progonomys–Occitanomys–Stephanomys* lineage were not drastic enough to directly control morphological evolution.

Our results therefore suggest an influence of both biotic and long-term abiotic changes on morphological evolution. These two types of interactions may not be exclusive and their interplay could finally explain the evolutionary patterns observed.

Evolution in size in the youngest deposits is clearly related to avoidance of interspecific competition between the two newly evolved species of the lineage. Morphological evolution along the whole lineage could also be related to the murine diversification, yet limited in Europe compared to Africa and Asia.

The development of stephanodonty and the correlated broadening of the molars, which allows a shift towards a more herbivorous diet, should

be selectively favored in the dry subtropical climate and more open landscape developing during the Late Miocene. Additionally, increasing size has been interpreted as allowing a better energetic control along the trophic chain, until reaching an optimum intermediate body size for mammals (Damuth, 1993). For small mammals like rodents, a trend towards increasing size could have been profitable in an arid and unpredictable climate.

The murine diversification itself could be a response to the changing environment. The trend towards dry subtropical conditions could open new ecological niches and therefore favor an adaptive radiation. In this case, the development of the dental specialization characteristic of our lineage would be a response to increasing competition, caused in turn by the long-term climatic trend.

4.4. *A model of interaction between environment and morphological evolution*

The general relationship between biotic and abiotic factors and microevolutionary patterns is still poorly understood. One of the main models of interaction between microevolution and environmental variations proposed so far is the 'Plus ça change' model (Sheldon, 1993, 1996). According to this model, stable periods would favor gradual evolution while highly perturbed periods would favor stasis interrupted by punctuated events of evolution, because periods of important environmental fluctuations would favor long-term generalist species which would usually survive without major changes.

Gradual evolutionary patterns along the *Progonomys–Occitanomys–Stephanomys* lineage fit the predictions of this model, since the Late Miocene period is not characterized by major environmental perturbations. This situation contrasts with the evolution of similar rodents in response to the Pliocene–Pleistocene major climatic shift (Renaud et al., 1999a), a major environmental perturbation that seems to have triggered an important and rapid morphological evolution. Huge environmental variations would eventually lead to accelerated morphological evolution, while during more stable periods evolution would occur

gradually, mainly as the result of biotic interactions such as interspecific competition.

5. Conclusion

The morphometric analysis of the molar outline along the murine lineage *Progonomys–Occitanomys–Stephanomys* confirms that size and shape of molars show gradual evolution. However, the rates of evolution of size and shape in first upper and lower molars are uncoupled.

Morphological evolution show a strong relationship with long-term climatic variations, suggesting that the Late Miocene trend towards a dry subtropical climate could have influenced the onset and development of morphological evolution along the lineage, by favoring the development of the stephanodont dental pattern allowing a more herbivorous diet. Such an abiotic influence could have been mediated by changes in the biotic interactions. Changing environment could have favored an adaptive radiation, leading to increased interspecific competition. These factors would have influenced size and shape evolution in the studied lineage, since morphological differentiation is a way of achieving niche partitioning in response to increased interspecific competition.

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