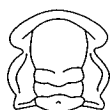


# Patterns of size and shape differentiation during the evolutionary radiation of the European Miocene murine rodents

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## LETHAIA



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Fourier analysis applied to the outlines of the first upper and lower molars of European Miocene murine rodents was used to quantify the size and shape variations associated with their radiation and to determine the evolutionary relationships among the taxa. The results suggested the occurrence of two lineages involving different evolutionary patterns. Size exhibits a rapid diversification in both lineages, probably because of selective pressures related to increasing competition among species. With regard to shape, one of the lineages is characterized by a conservative morphology, and the other by a tooth evolution oriented toward broader molars, which is interpreted as an adaptive specialization. Size and shape evolution are diversely associated during the radiation, and they may be related to the morphological differentiation of co-existing species and the avoidance of interspecific competition. □ *Fourier analysis, evolutionary trends, morphological variability, paleodiversity, Rodentia, Muridae, Miocene.*

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The investigation of trends in morphological evolution should improve understanding of the diversity of evolutionary patterns and give insight into the driving forces involved. Theoretical and quantitative approaches suggest that evolutionary trends may result either from adaptive forces or passive increase in variance of the clade (Stanley 1973; Gould 1988; McShea 1994). However, identifying these patterns in order to assess the adaptive forces involved requires detailed quantitative studies. Such studies of trends are still rare (Wagner 1996), although quantitative morphological analyses have been shown to be useful for analyzing macroevolutionary patterns in clades of invertebrates, such as trilobites (Foote 1993), or cladogenesis in micro-organisms (Lazarus 1986). A valuable case for an analysis of trends would be an evolutionary radiation, where several patterns of morphological evolution are expected to be found and to reflect a range of driving forces.

Although evolutionary radiations appear to be major features in the history of life, they have been mainly qualitatively described (Simpson 1944; Eisenberg 1981).

While a few quantitative studies are available concerning the morphological variations observed in such radiations (Foote 1995; Dommergues *et al.* 1996), these studies did not focus on the evolutionary pattern of the trends involved. Such an approach, however, would provide a better understanding of the mechanisms underlying the increase in morphological diversity that is expected to be associated with the increase in biodiversity during a radiation.

An example may be provided by European Miocene murine rodents (subfamily Murinae, family Muridae). This group emerged during the Late Miocene from *Antemus chinjiensis*, a Middle Miocene Indian rodent which is considered to be the oldest and most primitive murine (Jacobs 1977). Already differentiated from *Antemus*, the first murines are recorded in Europe from the beginning of the Late Miocene, at about 11 Ma (Aguilar & Michaux 1996). Two species were present at that time, *Progonomys hispanicus* and *Pr. cathalai*, which display overlapping distribution areas in southwestern Europe. Following this phase of immigration, a diversification occurred with the

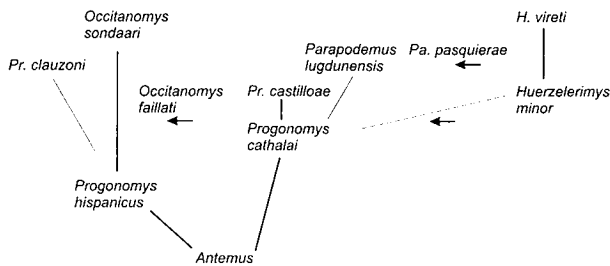


Fig. 1. Phyletic relationships of the murines in southern France at the beginning of the Upper Miocene, modified after Michaux (1971), Mein *et al.* (1993), Aguilar & Michaux (1996) and Michaux *et al.* (1997). Thick line: undebated ancestor–descendant relationships. Thin line: ancestor–descendant relationships proposed by Michaux (1971) and questioned by Aguilar & Michaux (1996) and Michaux *et al.* (1997). Dashed line: ancestor–descendant relationships of Michaux (1971) and Mein *et al.* (1993) but interpreted as immigration in southwestern Europe from an undetermined origin by Aguilar & Michaux (1996) and Michaux *et al.* (1997). Arrows: immigration in southwestern Europe from an undetermined origin (Aguilar & Michaux 1996; Michaux *et al.* 1997).

appearance of the new genera *Occitanomys*, *Parapodemus*, and *Huerzelerimys*. From *Occitanomys* would emerge *Stephanomys*. The dental morphology of this genus is particular and typifies a specialization named ‘stephanodonty’ (Schaub 1938; Misonne 1969), which is characterized by the development of longitudinal crests joining the cusps in a garland-like dental pattern on the upper molar. It has been interpreted as an adaptation to a more abrasive diet, probably grass (Michaux 1978; Denys 1994). Compared to *Occitanomys* and *Stephanomys*, the genera related to *Parapodemus* have a more classical murine dental pattern which should have been associated with the usual omnivorous–granivorous murine diet. Finally, *Huerzelerimys* is characterized by a considerable size increase through time.

This diversification of the European Miocene murines has been previously studied using traditional methods in vertebrate paleontology, i.e. size comparisons of the teeth and comparative descriptions of the detailed tooth morphology. This approach led to the definition of numerous species (Fig. 1), although the mechanisms involved in this diversification are still debated. This diversification has formerly been interpreted as a consequence of a local radiation in southwestern Europe (Michaux 1971; Van de Weerd 1976), while recent interpretations, based on the description of an increasing number of sites and species, involved several migratory waves into southwestern Europe from an undetermined origin (Aguilar & Michaux 1996; Michaux *et al.* 1997). This uncertainty in the evolutionary interpretation may be due to the fact that the methods employed can only qualitatively describe the differences in shape between the taxa; they do not allow quantification of the amount of divergence existing

between them, and are, thus, dependent on subjective interpretations. We use here a Fourier analysis method, which lets us quantify the differences in shape by analyzing the two-dimensional outline of the tooth. Its application to the radiation of the European Miocene murines allows us (1) to assess quantitatively the morphological divergence of the different taxa and potentially clarify the mechanisms involved in the diversification; (2) to compare the evolutionary patterns of both shape and size; and (3) to assess the relation between these evolutionary patterns and the increase in biodiversity during the radiation.

## Material and methods

### Material

We analyzed 431 first upper molars and 445 first lower molars of Miocene murines from nine deposits of seven French mammal-bearing localities (Fig. 2). Several genera and species of murines have been identified in these localities. In the absence of any clear evidence of artefactual mixing of fossils, the co-existence of several species in one locality is regarded as indicative of a paleocommunity. A summary of the composition, sample size, and corresponding reference for each locality is provided in Table 1.

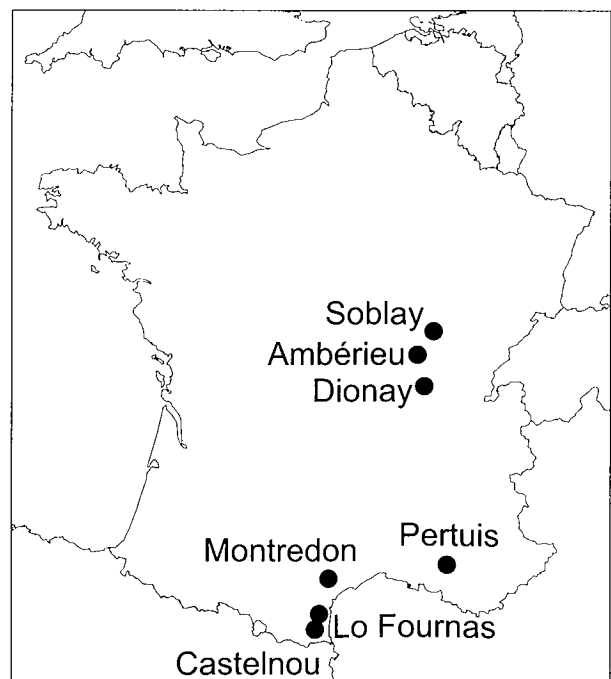


Fig. 2. Location of the different fossil mammal-bearing localities of the study.

Table 1. Composition, sample size of the first upper molars (lower molars), and corresponding references for the different deposits studied. RA: relative ages (order of succession) of the fossil mammal-bearing localities. Ma: approximative absolute ages in million years. MN: Mammals Neogene zones. Three samples from the deposit of Montredon were available: upper level 1 (u.l.1), upper level 2 (u.l.2), and lower level (l.l.). References: Jacobs 1978 (A); Aguilar 1981 (P); Aguilar 1982 (M1, M2, M3, C); Mein 1984 (D, S); Farjanel & Mein 1984 (A1, A2); Aguilar *et al.* 1986 (F6, F7).

Ma	MN	RA	Code	Deposits	<i>Ante-</i> <i>mus</i>	<i>Progonomys</i> <i>hispa-</i> <i>nicus</i>	<i>catha-</i> <i>lai</i>	<i>castil-</i> <i>loac</i>	<i>clau-</i> <i>zoni</i>	sp.	<i>Huerzelerimys</i> <i>vireti</i>	<i>Parapodemus</i> <i>lugdun-</i> <i>ensis</i>	<i>pasqui-</i> <i>erae</i>	<i>Occitanomys</i> <i>faillati</i> <i>son-</i> <i>daari</i>
8.5	11	7	P	Pertuis										5(3)
	10/11	6	D	Dionay		15(15)			24(16)	1(-)	41(44)	18(20)		
		5	A2	Ambérieu 2c							17(12)	16(10)		
		5	F6	Lo Fournas 6					67(72)				25(22)	
		4	A1	Ambérieu 1			4(2)		5(7)			25(16)		
	10	4	F7	Lo Fournas 7				46 (49)			3(3)			1(1)
		3	S	Soblay			38(38)							
		3	M1	Montredon u.l.1			36(40)							
		3	M2	Montredon u.l.2			32(64)							
		3	M3	Montredon l.l.			11(11)							
11.5	9	2	C	Castelnou 1b		1(-)								
12-14	8	1	A	Siwalik	2(-)									

In order to compare the morphology of these European Miocene murines to the ancestral morphology, we also included in our analysis two upper molars of the most primitive murine, *Antemus chinjiensis*, from the Siwalik (Pakistan) and dated about 12–14 Ma (Jacobs 1978).

Deposits are dated using a biochronology based on several independent rodent lineages. As the dating of such continental deposits are difficult to correlate with an absolute time scale, only the order of succession has been considered here, providing a relative age for each deposit (R.A. in Table 1).

#### Fourier analysis of the outline

Two morphometrical approaches are available to describe the morphology of the tooth: landmarks and outline analysis. Previous qualitative studies have focused on the location and size of the different tubercles as well as the presence and development of enamel crests between the tubercles. These qualitative studies are not suitable for the accurate description of the latter characters, which, nevertheless, may only be morphological epiphenomena when compared to the overall morphology of the tooth. Landmark-based methods were considered unsuitable in the present analysis because (1) defining the same set of landmarks for all the taxa was difficult, since additional tubercles appeared in some species; (2) the location of landmarks on tubercles and crests is particularly sensitive to modifications of the occlusal surface due to tooth wear (Van Dam 1996). On the other hand, although not directly related to the characters used in the previous taxonomic studies, the outline describes the overall morphology of the tooth and especially the position of the main tubercles, which appear as bulges on the outline. Additionally, outlines, even complex ones, can be described in a very simple way using a Fourier method

(Foote 1989). This method also allows us to limit the influence of measurement error by filtering the noise occurring on details of the outline.

The outline analyzed corresponds to a 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 (OPTIMAS v.4.0). 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 were calculated corresponding to the distance of each of the points to the center of gravity of the tooth. A discrete Fourier analysis was then applied to this set of 64 radii, expressed as a function of the cumulative distance along the outline (Renaud, in press; Renaud & Girard 1999). The outline is thus expressed as a finite sum of trigonometric functions of decreasing wave length, i.e. the harmonics, according to the formula (Wolfram 1991):

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

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 order of the harmonic. Each outline can therefore be described by a set of Fourier coefficients  $a_n$  and  $b_n$ .

The size was standardized by dividing all the coefficients by the 0th harmonic amplitude,  $a_0$ , which is the diameter of the best-fit circle to the digitized outline and can thus be used as a measure of size (Ehrlich & 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 & Archie 1984).

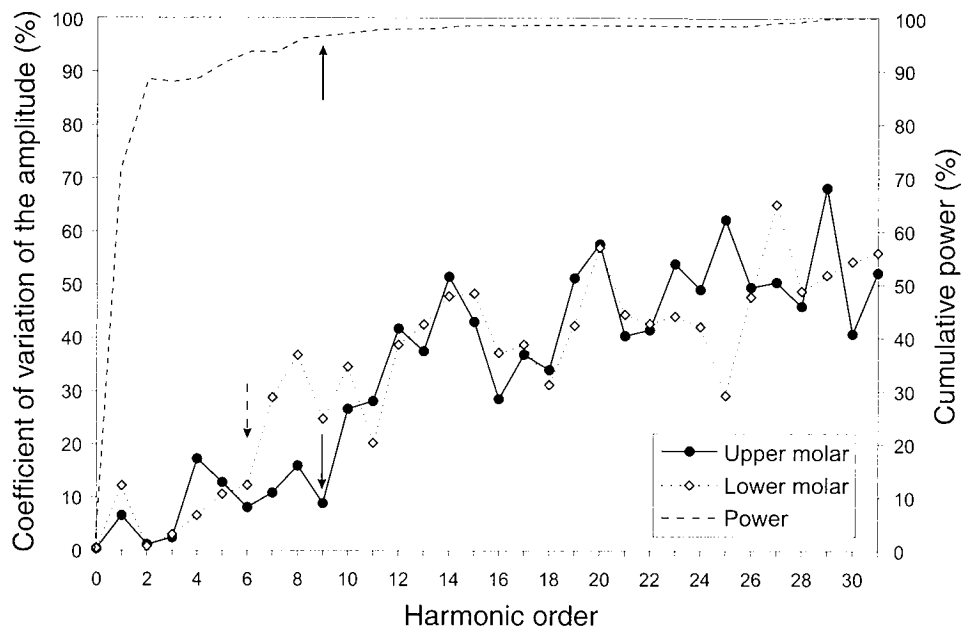


Fig. 3. Measurement error and cumulative power as a function of the harmonic order. The measurement error is expressed as the mean coefficient of variation of the harmonic amplitude ( $= \sqrt{a_n + b_n}$ ) of five specimens measured five times. Cumulative power (dashed line) corresponds to the deviation of reconstructed outlines based on increasing numbers of harmonics from the reconstruction based on the maximum number of harmonics ( $H = 31$ ), for an upper molar. The arrows indicate the threshold order for the upper molar (full line) and the lower molar (dotted line).

A characteristic of the Fourier harmonics is that the higher the order of the harmonic, the more details of the outline it describes. This property can be used to filter measurement noise as it is expected to increase with the harmonic order (Renaud *et al.* 1996). Thus, the effect of noise was detected by expressing the measurement error as a function of the harmonic order. Measurement error was estimated by five repeated measurements of five specimens and expressed as the mean coefficient of variation of the harmonic amplitude ( $= \sqrt{a_n + b_n}$ ). Results indicated an increase in measurement error with the harmonic order as predicted (Fig. 3), with an important increase at the ninth harmonic for the upper molars and at the sixth harmonic for the lower molars. Above these threshold harmonics, the measurement error reached values greater than 20% of the signal, which may render the Fourier coefficients unreliable. The content of information added by each harmonic has also been estimated using the cumulative power (Cramton 1995) as a function of the harmonic order (Fig. 3). For the upper molars, 90% of the total power is reached at the sixth harmonic and 95% at the ninth harmonic. For further analyses, Fourier coefficients have, therefore, been considered up to the ninth harmonic for the upper molars and up to the sixth for the lower molars. These threshold values provide a good compromise between the informative content and the limitation of the measurement error.

Note that the measurement error increased faster for the lower molars than for the upper molars. This may be due to the fact that the outline of the lower molar is more roughly trapezoidal and displays less characteristic features than that of the upper molar. Since the definition of

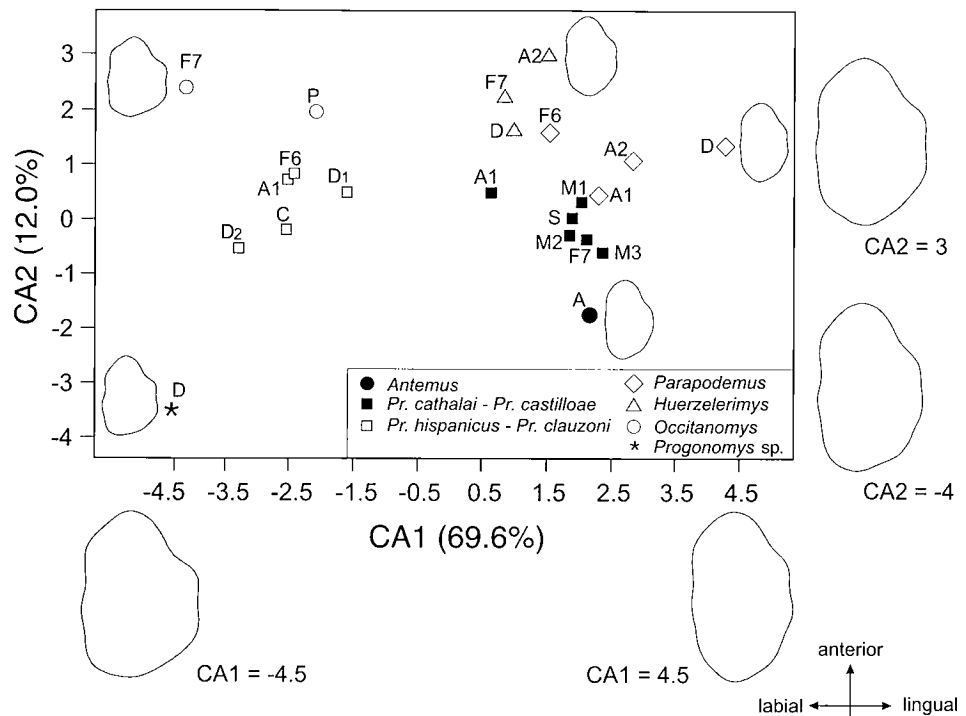
the starting point was also less accurate, only the harmonic amplitudes, which are independent of the starting point, were used for the morphometric analysis of the lower molars. In this case, the outline could not be reconstructed with the inverse Fourier transform.

#### MANOVA on the Fourier coefficients

A set of 18 coefficients and 6 amplitudes was obtained for each upper and lower molar, respectively. A MANOVA (multivariate analysis of variance) was performed on these variables using NTSYS-pc (Rohlf 1993) in order to display the relationships among group means relative to within-group variation. In our analysis, the groups correspond to the different samples of each fossil species in the different deposits. A canonical variate analysis is also performed associated with the MANOVA. A test of significance for differences among group means is provided (Wilk's Lambda test), as well as the scores of the group means along the canonical axes (Marcus 1993). In this space describing the variation in morphology, the relative position of each sample, corresponding to different species and different deposits, can be visualized independently of their relative age.

MANOVAs and canonical variate analyses were computed considering only the groups with more than five molars and the sample of *Antemus*. Group means of small samples with less than five teeth were considered insufficiently reliable to be included in the analysis. Therefore, their coordinates in the canonical space were calculated afterwards using the canonical vectors.

Fig. 4. First two canonical axes and corresponding outlines for the upper molar. The labels correspond to the deposit code (Table 1). For Dionay (code D): D<sub>1</sub>, *Pr. hispanicus*; D<sub>2</sub>, *Pr. clauzoni*. The reconstructed outlines are obtained using inverse Fourier transform on sets of coordinates along the canonical vectors. Mean outlines corresponding to some of the groups have been added.



## Results and discussion

### Patterns of morphological differentiation

The MANOVA on the Fourier coefficients  $a_n$  and  $b_n$  of the first upper molar indicates a morphological differentiation among groups (Wilk's Lambda = 0.033;  $df_1 = 5.785$ ;  $df_2 = 270$ ;  $P < 0.001$ ). The position of the different groups in the canonical space, with the most variation explained by the first canonical axis (69.9% of the among-group variance), contrasts one group including *Progonomys hispanicus*, *Pr. clauzoni*, and *Occitanomys*, with another one including all the *Progonomys cathalal*, *Pr. castilloae*, *Parapodemus* and *Huerzelerimys* (Fig. 4). In the latter group, a subdivision clusters five of the samples together, corresponding to *Pa. pasquierae* (F6), *Huerzelerimys* and the *Pr. cathalal* from A1. The second axis (only 12.0% of among-group variance) mainly separates the European Miocene murines from their ancestor *Antemus*, which seems to be morphologically closer to the *Pr. cathalal* group than to the *Pr. hispanicus* one. The reliability of the method is supported by the clustering of the three samples from Montredon (M1, M2, and M3), and by the coherence between the location of the groups with a small sample size, which were added as supplementary groups, and their previous identification. The sample from Castelnou 1b (C), the oldest *Pr. hispanicus* in the study, is grouped with the other *Progonomys* of the *Pr. hispanicus* group. *Occitanomys faillati* from Lo Fournas 7 (F7) have an extreme position in the *Pr. hispanicus* group, suggest-

ing that their morphology should be the most derived in this group. *Huerzelerimys vireti* from F7 are located near the other *Huerzelerimys*. *Progonomys* aff. *cathalal* from A1, although close to the *Pr. cathalal* group, seem to be morphologically more related to the group of *Huerzelerimys*, suggesting that *Progonomys cathalal* could be an ancestor of the genus *Huerzelerimys*. Finally, the *Pr.* sp. from Dionay (D), although having an extreme location along the second canonical axis, seems closer to the *Pr. hispanicus* group on the basis of its position along the first canonical axis.

The reconstruction of mean outlines corresponding to some of the groups, as well as the theoretical outlines corresponding to the coordinates along the canonical axes, demonstrate the differences involved in this shape differentiation (Fig. 4). The first canonical axis clearly contrasts a narrow elongated tooth, characteristic of the *Pr. cathalal* group, with a broad tooth, with a flat posterior part and a very concave shape at the lingual anterior part, characteristic of the *Pr. hispanicus* group. *Antemus* is especially characterized by a protuberant tubercle at the labial posterior part of the tooth, which could be considered as a primitive character inherited from its cricetid ancestor (Wessels *et al.* 1982); its narrow outline is otherwise more related to *Pr. cathalal* than to *Pr. hispanicus* and *Occitanomys*.

Following the same method, a MANOVA was also carried out on the Fourier amplitudes of the first lower molar. The groups were morphologically differentiated

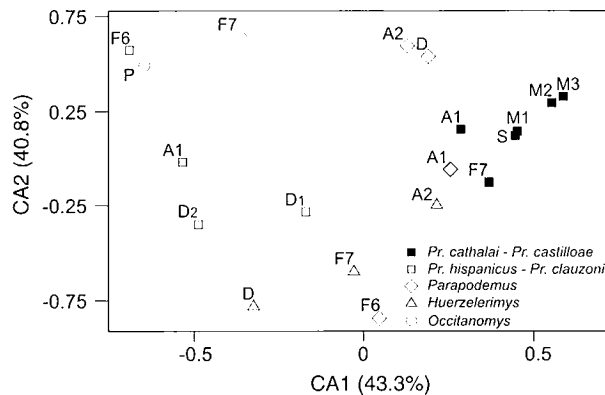


Fig. 5. First two canonical axes for the lower molar. The labels correspond to the deposit code (Table 1). For Dionay (code D): D<sub>1</sub>, *Pr. hispanicus*; D<sub>2</sub>, *Pr. clauzoni*.

similarly to the upper molars (Wilk's Lambda = 0.629;  $df1 = 8.635$ ;  $df2 = 24$ ;  $P < 0.001$ ). The same clear differentiation between the *Pr. hispanicus* group and the *Pr. cathalal* one as is seen on the upper molars emerges here (Fig. 5). The youngest *Parapodemus lugdunensis* (A2 and D) are morphologically differentiated from *Pr. cathalal*; the different samples of *Huerzelerimys* are intermediate between the two main groups, and *Pa. pasquierae* from F6 are closer to *Huerzelerimys* than to the other *Parapodemus*. The latter observation suggests that the attribution of *Pa. pasquierae* to *Parapodemus* should be reconsidered, as this species may belong to *Huerzelerimys*. Furthermore, the distinction between *Pr. cathalal* and *Pr. castilloae* is not detected by the present morphometric analysis.

As with the upper molar, the groups with small sample sizes have coherent locations in the canonical space. The *Huerzelerimys* from F7 are located close to the other *Huerzelerimys*, as are the *Occitanomys* from F7 to the other *Occitanomys* samples. Noteworthy, the *Pr. cathalal* from A1 are near other samples of this species, whereas for the upper molars, they were closer to the *Huerzelerimys* group than to the other *Pr. cathalal*.

Although differences exist between the morphological relationships displayed by the upper and lower molars, a Mantel test on the distances between among-group means of the upper molars and those of the lower molars in the canonical spaces ( $r = 0.238$ , Mantel  $t = 1.757$ ,  $P = 0.039$ ) shows that they are significantly correlated.

### Evidence for a European radiation of the Upper Miocene murines

From these results emerged two distinct morphological groups, the *Pr. hispanicus* and the *Pr. cathalal* groups. This evidence does not support the hypothesis of recurrent immigrations from a distant origin, since the morpholog-

ical homogeneity of the two groups would imply a parallel evolution of the two European groups and of the immigrant stock, although they were genetically isolated and subjected to different environmental pressures. It seems more parsimonious to envisage the morphological homogeneity of the European murines as a consequence of an in situ radiation in Europe. In this case, the relationships proposed in recent paleontological studies (Aguilar & Michaux 1996; Michaux *et al.* 1997) have to be understood as an interpretation of the local southwestern European fossil record, with some arrivals of members of the same main lineages but from another area within Europe. The two main morphological groups can thus be interpreted as the members of two branching lineages.

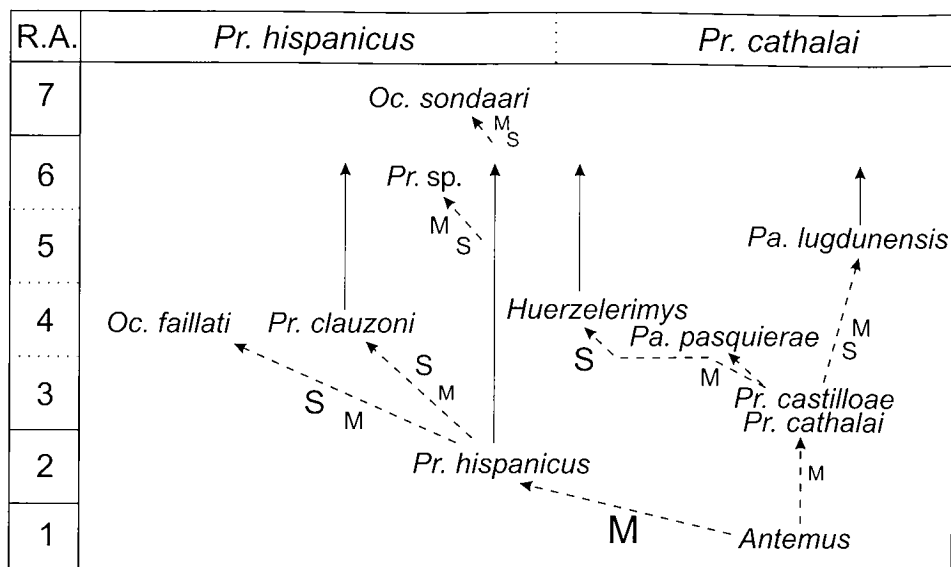
Finally, it should be noted that from a taxonomic point of view, the relationships between the different taxa deduced from these morphometric analyses (Fig. 6) appear to be close of the previous taxonomic interpretations (Fig. 1) but provide more detail to resolve the problems and discussions existing about the relationships between taxa. It also raises again the question about the taxonomy of the genus *Progonomys*, with Aguilar & Michaux (1996) and Michaux *et al.* (1997) defining *Progonomys* as the primitive stage of evolution in the whole lineage, while Mein *et al.* (1993) consider that the term *Progonomys* should be reserved to the *Pr. cathalal* – *Parapodemus* clade, a view supported by the wide morphological divergence between the lineages of *Pr. hispanicus* and *Pr. cathalal*.

### Evolution of size and shape

Studying the evolutionary processes involved in the morphological differentiation between these two lineages requires the introduction of the time dimension as well as comparison of size and shape, which, when taken together, describe the whole form. For this purpose, we focus on the upper molar, which seems to be better differentiated and less sensitive to measurement error than the lower molar. The first canonical axis, accounting for almost 70% of the variance, was chosen as the shape variable. The 0th harmonic amplitude,  $a_0$ , proportional to the size of each tooth, was chosen as the size variable. Time is expressed as the order of succession of the localities (R.A. in Table 1).

Size and shape of the upper molar (Fig. 7A) show a globally uncorrelated evolution (coefficient of correlation:  $R^2 = 0.24$ ,  $P = 0.491$ ). However, the relationship between these variables appears to be different when both lineages are considered independently. The lineage leading from *Antemus* to *Pr. cathalal* and then to *Parapodemus* and *Huerzelerimys* exhibits a correlated evolution of morphology with size, following an allometric power function ( $a_0 = 6.8 \text{ CA1}^{-0.2}$ ,  $R_2 = 0.58$ ,  $P < 0.001$ ). The pattern in the lineage derived from *Pr. hispanicus* seems different but

Fig. 6. Hypothetical relationships between the Upper Miocene European murines according to the present study. Full arrows show continuation of the corresponding species; dotted arrows are speciation events, S is a size variation, M a shape variation (the font size is roughly proportional to the amount of variation occurring during the speciation).



depends on the confidence accorded to the single specimen of *Pr. sp.* from Dionay. If the corresponding data point is considered as valid, size and shape in this lineage appear to be uncorrelated ( $R^2 = 0.22$ ,  $P = 0.725$ ), whereas if the *Pr. sp.* from Dionay is discarded as an aberrant specimen related to *Pr. hispanicus*, size and shape are weakly correlated ( $R^2 = 0.70$ ,  $P = 0.019$ ). It would seem that the relationship between size and shape is weakened in the *Pr. hispanicus* lineage.

The evolutionary patterns within these lineages were visualized by plotting size and shape against time. The evolution of the shape (Fig. 7B) shows that the two main lineages have different evolutionary patterns. The first lineage leads from *Antemus* to *Progonomys cathaloi* with minor shape changes; then a morphological differentiation, which can be interpreted as a cladogenesis, occurs, leading to *Huerzelerimys* on one hand and to *Pa. lugdunensis* on the other. The second main lineage is the lineage derived from *Pr. hispanicus*. The sample from Castelnou 1b (C), corresponding to the first occurrence of this lineage, appears to be already highly differentiated from the ancestral morphology of *Antemus*. This morphological difference with the lineage *Antemus* – *Pr. cathaloi* is conserved later on during the morphological diversification characterizing the lineage of *Pr. hispanicus* since R.A. 4. This period represents also the beginning of the morphological diversification in the lineage of *Pr. cathaloi* and seems to correspond to the start of the radiation itself.

The evolutionary pattern of size (Fig. 7C) shows a stage of stasis in the deposits just consecutive to the immigration into Europe of *Pr. hispanicus* and *Pr. cathaloi* (R.A. 2 and 3), followed by a progressive diversification of the size range, beginning, as for the shape, at the time of R.A. 4. Although an increase in size is the dominant trend, char-

acteristic of *Pr. clauzoni*, *Occitanomys faillati* and *Huerzelerimys*, all trends in size evolution can be found. Stasis characterizes the lineage *Pr. cathaloi* – *Parapodemus lugdunensis* from Montredon (M) up to Ambérieu 2c (A2), while a decrease in size occurs leading to *Pa. lugdunensis* and possibly to *Pr. sp.* from Dionay (D).

#### Driven and passive evolutionary trends

This pattern of size differentiation, starting from the relatively small *Antemus*, is characterized by a large increase in size of the largest species and a slight decrease in size of the smallest species present at the same time. This pattern of size differentiation clearly fits that expected for an increase of variance in size in a trend starting from a small ancestor, with a lower bound on size (Stanley 1973; Gould 1988). Increases and decreases in size should thus occur about equally often, and only the existence of a constraint on the minimum size explains the asymmetrical pattern of diversification. This kind of pattern can be termed a *passive system* (McShea 1994) and has previously been found in rodents on a larger scale (Stanley 1973). The present example shows that this passive increase in size range may also explain the evolutionary patterns of size at a finer scale.

The shape differentiation (Fig. 7B) appears to be driven by different mechanisms. The morphologically conservative lineage of *Pr. cathaloi* appears to have a symmetrical increase of variance. This would also correspond to a passive system, but without a bound limiting the diversification in a given direction. The existence of an allometric relationship between size and shape in this lineage suggests that differentiation in shape may be related to diversification in size. The pattern is quite different in the lin-

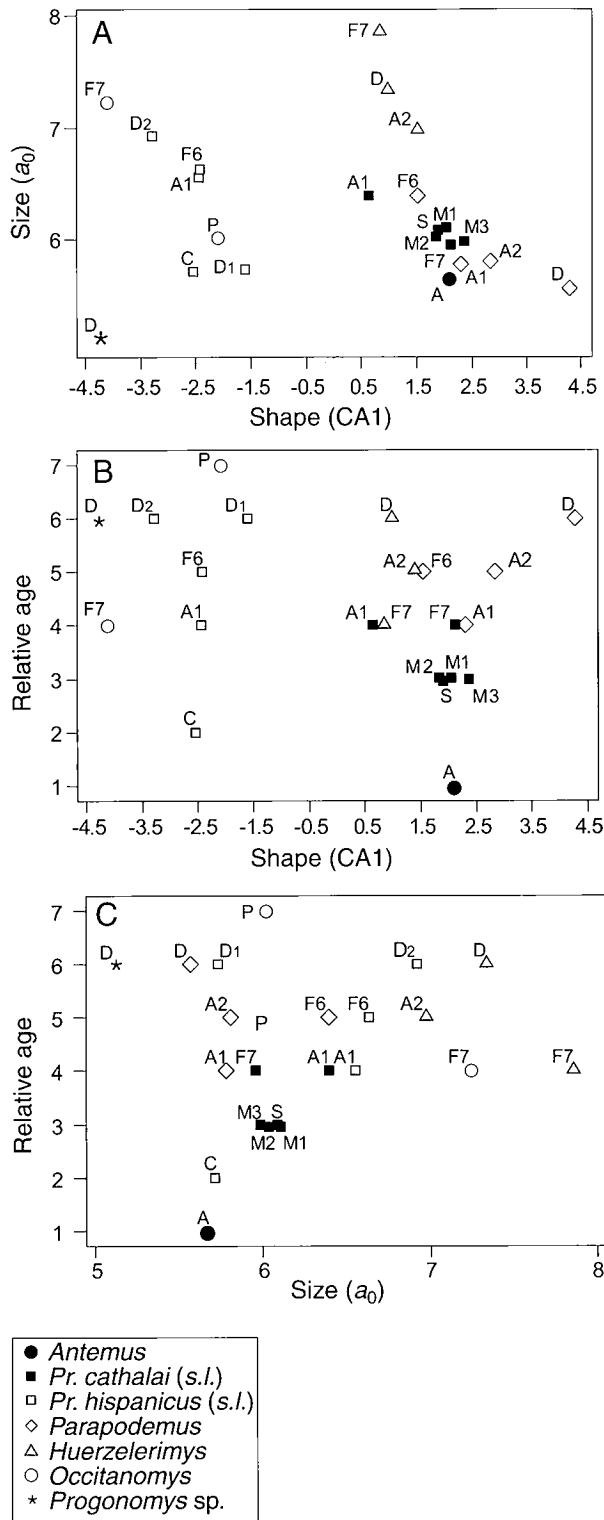


Fig. 7. Plots illustrating the evolution of shape and size for the upper molar. □A. Shape vs. size. B. □Shape vs. time. □C. Size vs. time. Shape is expressed as the coordinates of group means along the first canonical axis; size is expressed by the 0th harmonic amplitude  $a_0$ ; the time variable corresponds to the order of succession of the deposits (R.A. in Table 1).

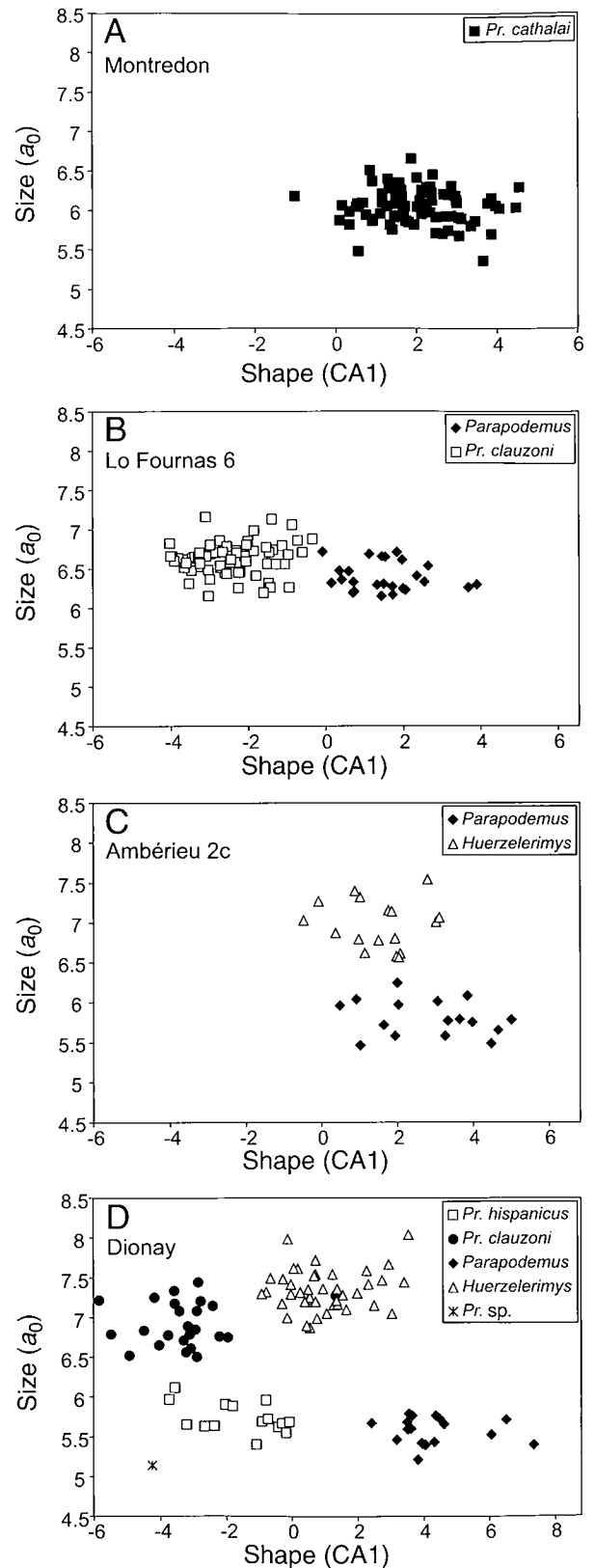


Fig. 8. Variability in size and shape of the upper molar plotted for different deposits. Shape is expressed as the coordinates along the first canonical axis, and size by the 0th harmonic amplitude  $a_0$ . A = R.A. 3; B and C = R.A. 5; D = R.A. 6.



Table 2. Differentiation in size and shape within the deposits of Dionay, Ambérieu 2c and Lo Fournas 6. For each pair of species within these deposits, the size differentiation has been tested using an ANOVA on  $a_0$ , and the shape differentiation using a MANOVA on the Fourier coefficients.

			<i>Progonomys clauzoni</i>	<i>Huerzelerimys minor</i>	<i>Parapodemus lugdunensis</i>	<i>Parapodemus pasquierae</i>
Dionay	<i>Progonomys hispanicus</i>	Size	0.000	0.000	0.011	
		Shape	0.002	0.000	0.000	
	<i>Progonomys clauzoni</i>	Size		0.000	0.000	
		Shape		0.000	0.000	
	<i>Huerzelerimys minor</i>	Size			0.000	
		Shape			0.000	
Ambérieu 2c	<i>Huerzelerimys minor</i>	Size			0.000	
		Shape			0.000	
Lo Fournas 6	<i>Progonomys clauzoni</i>	Size				0.000
		Shape				0.000

eage of *Pr. hispanicus*. From the beginning, this lineage is characterized by molars broader than those of the ancestor *Antemus* and the *Pr. cathalai* lineage. This morphological difference tends to increase in the new species of the lineage of *Pr. hispanicus*. This bias towards broader molars in new species would correspond to the definition of a driven trend (Foote 1993; McShea 1994; Wagner 1996), owing to an evolutionary pressure favoring broader morphotypes. However, this hypothesis can hardly be tested within the time range of this study, which is too short to measure the displacement of the minimum of the distribution towards broader molars, as expected in driven trends (McShea 1994).

### Biodiversity and morphological variability

An evolutionary radiation is a period of strong increase in biodiversity within a group. Following the ecological-niche theory (Hutchinson 1959), the distribution of species should be influenced by the mosaic of potential niches offered by the environment. If the morphology is related to the ecological distribution, we may expect that the distribution of the species will not overlap in a morphospace, corresponding to the partition of niches among species (Schoener 1974), and the increase in biodiversity associated with the radiation will depend on this resource partitioning.

This hypothesis can be tested on the deposits with large sample sizes for all the co-existing species, i.e. Lo Fournas 6 (F6), Ambérieu 2c (A2) and Dionay (D). Within each of these deposits, shape differentiation has been tested by MANOVA on the Fourier coefficients of the different pairs of species, and size differentiation by ANOVA on the size variable  $a_0$  (Table 2). Each pair of species displays a significant differentiation in both size and shape, but the level of differentiation observed between two species can vary according to the character considered (deposit of Dionay, Table 2). Therefore, in order to fully understand the importance of the evolutionary patterns of size and shape in the context of an evolutionary radiation, we have

to look at the diversity of size and shape within each deposit, and the evolution of this diversity through time.

For this purpose the Fourier coefficients of all the individuals were projected onto the canonical space, and the coordinates of each outline on the first canonical axis was considered, as previously, as the shape variable. This shape variable was then plotted against size for four deposits rich in material and representing the different steps in the radiation (Fig. 8). In Montredon (Fig. 8A), the oldest deposit, only one species (*Pr. cathalai*) is present. In the following deposits of Lo Fournas 6 and Ambérieu 2c, the biodiversity has already increased and two species are present. In Lo Fournas 6 (Fig. 8B), both species are approximately of the same size, but *Pr. clauzoni* and *Pa. pasquierae* are separated by the morphological differentiation inherited from their ancestors, *Pr. hispanicus* and *Pr. cathalai*, respectively. The pattern is different in Ambérieu 2c (Fig. 8C), where the two species have a similar morphology, both of them belonging to the *Pr. cathalai* group (Fig. 4). They are still segregated in the morphospace, but this time mostly along the size axis. The deposit of Dionay (Fig. 8D), one of the youngest deposits of this study, shows the greatest biodiversity, and the species are segregated in the morphospace along both the size and the shape axes. The shape axis differentiates members of the two main morphological groups, within which the species are further differentiated by a divergence in size.

These patterns fit the hypothesis of resource partitioning through size and shape differentiation. As molar size is a good estimate of body size for rodents (Legendre 1989), and as body size is related to differences in ecological characteristics such as micro-habitats and feeding habits (Hutchinson 1959), the differentiation in size may limit inter-specific competition (Dayan *et al.* 1990), and thus be a factor favoring the increase in biodiversity during the radiation.

Determining the significance of shape variation is less obvious, but its role in avoiding competition between sympatric species has also been evoked (Dayan & Simberloff 1994). The broadening of the molars in the *Pr. hispan-*

icus group may be related to the acquisition of a specialized dental pattern, since this emerging lineage is characterized by the appearance and progressive improvement of stephanodonty. This specialization corresponds to the development of longitudinal crests on the upper molars, sliding in a corresponding groove of the lower molars. As this structure improves the grating function of the murine dentition, it has been interpreted as an adaptation to a more abrasive and herbivorous diet (Michaux 1978; Denys 1994). The broadening of the molars observed in the lineage may be related to this development of longitudinal crests. The morphological trend towards broad molars may thus be adaptive, leading to competition avoidance with species of a similar size but with unspecialized dental morphology, as seen in the *Pr. cathalai* lineage.

## Conclusions

The different patterns observed for size and shape, and for the different main lineages, suggest that evolutionary driving forces underlying the evolutionary radiation of the European murine rodents are complex and multiple, varying with the character and the lineage considered. The discrepancy between evolutionary patterns of size and shape have already been noted (Hallam 1978; Renaud *et al.* 1996) and seems here to be attributable to a different range of factors acting on size and shape. Size appears to be ruled essentially by ecological factors, such as competition among species, whereas shape could be influenced either by allometric processes or by functional adaptive factors such as the acquisition of a new dental pattern. The evolutionary pattern of shape of the *Pr. hispanicus* lineage may be an adaptive trend characterized by an increase in variability corresponding to the preferential appearance of derived morphologies, while the diversification of the *Pr. cathalai* lineage may be only due to passive diffusion through the morphospace, with no morphological innovation leading the lineage in a particular direction. This discrepancy between both lineages underlines that the relationship between traits such as size and shape, strongly allometrically coupled in one lineage, may be disturbed if one of the traits is subjected to a new range of selective pressures, such as the acquisition and improvement of a new dental pattern (McKinney 1990).

Therefore, the evolutionary patterns observed will depend not only on the characters considered, such as size and shape, but also on the lineage considered. A detailed analysis of the evolutionary patterns is required in order to identify the processes underlying the evolution and assess the frequency of active trends relative to passive increases in morphological diversity.

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