



# Size and shape variability in relation to species differences and climatic gradients in the African rodent *Oenomys*

Sabrina Renaud *Institut des Sciences de l'Evolution, CC064, Université Montpellier II, F-34095 Montpellier Cedex 05, France*

## Abstract

**Aim** The modern African murine rodent *Oenomys* is a semiarboreal genus characteristic of the rain forest zone. The size and shape geographical differentiation is studied in order to discuss the possible evolutionary patterns and constraints leading to this distribution.

**Location** Two species of *Oenomys* have been previously recognized, corresponding to the West African forest block on the one hand and to the main forest block on the other hand. Both species have been sampled, and forty localities permit the study of the whole geographical range of *Oenomys*, from Guinea to Kenya.

**Methods** A Fourier analysis applied to the outlines of the first upper and lower molars allows a quantification of the size and shape variations across the geographical range of *Oenomys*.

**Results** This morphometrical analysis defines three morphological groups of *Oenomys*, corresponding to the West, Central, and East African forest zone. This result suggests the existence of an additional cryptic species. The Western group is characterized by broad asymmetrical molars and a small size. The Central African group has more elongated and larger molars while the Eastern African group displays extremely constricted molars and a small size.

**Main conclusion** The shape can be considered as characteristic of each group and its variations appear to be mostly related to phylogeny while size exhibits variations within each group related to climatic gradients. This discrepancy could be related to different genetic determinants for both characters, the shape being strongly genetically constrained while size can vary according to a wide range of environmental factors.

## Keywords

Fourier analysis, geographical variation, Muridae, morphology, evolution.

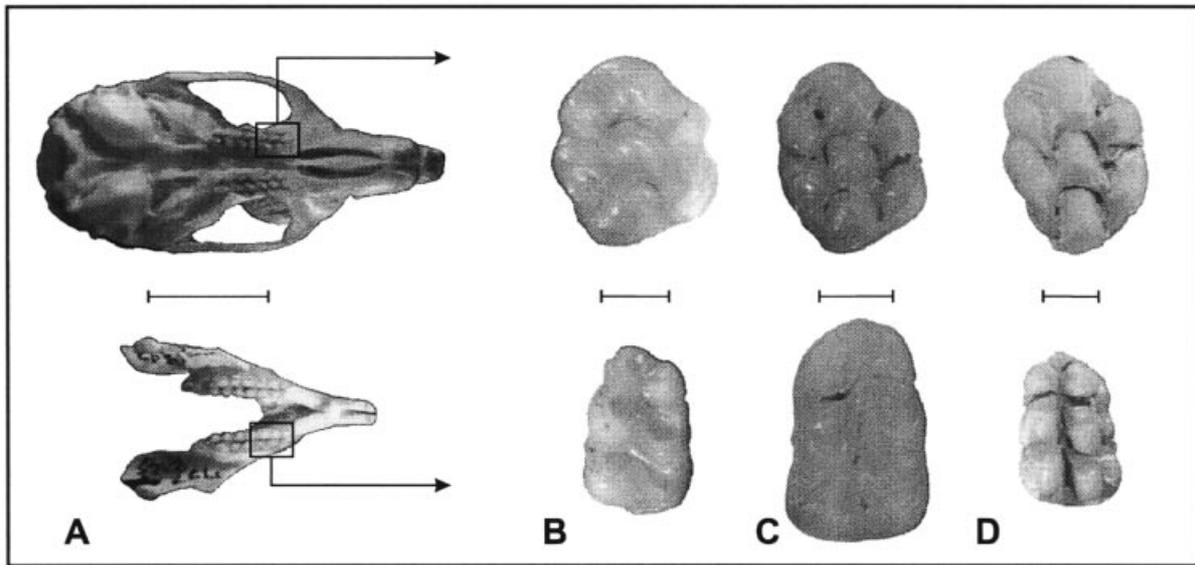
## INTRODUCTION

In order to improve our understanding of evolutionary processes, a detailed comprehension of the biogeography of extant species is required as well as a study of the evolution of extinct species through the fossil record. Modern species are the only model where evolutionary hypotheses based on a morphological analysis can be tested by a molecular approach, and where comprehensive sampling is possible compared to the often scarce fossil record. Finally, the complex relationships between morphological variation and phylogenetic constraint

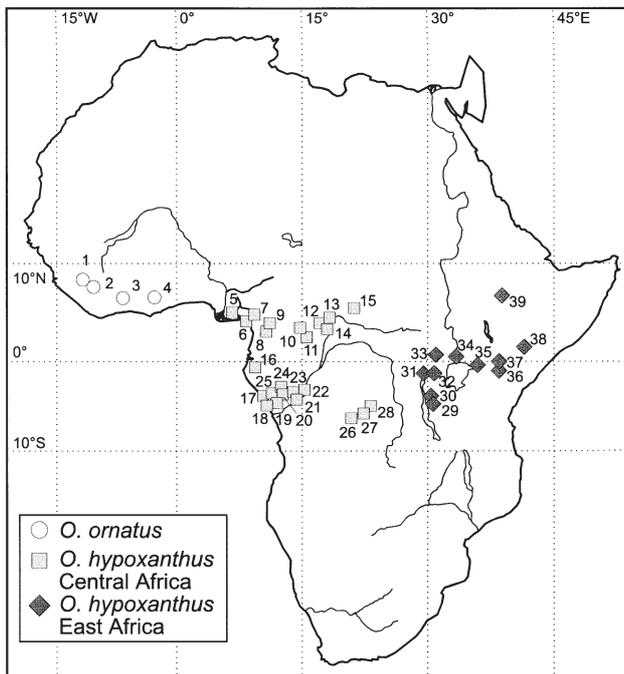
on one hand and environmental variation on the other hand can be more easily deciphered on modern species. Detailed studies of the biogeographic patterns of morphological variation can therefore provide precious clues for interpreting evolutionary patterns of fossil or extant species.

The modern African murine rodent, *Oenomys* Thomas 1904 (Fig. 1) ranges from south-east Guinea through the Congo forests to Uganda and Kenya (Fig. 2). *Oenomys* is characteristic of the rain forest zone, although it lives in open areas with dense undergrowth and grass (Rosevear, 1969). In East Africa, its favourite habitat is mountain forest up to 3000 m in elevation with a broken canopy and dense undergrowth (Kingdon, 1974). This murine exhibits a dental specialization named 'stephanodonty' (Schaub, 1938; Misonne, 1969), which is characterized by the development of longitudinal crests joining

Correspondence and current address: Centre de Paléontologie Stratigraphique et Paléocologie, CNRS-UCBL, Université Lyon 1, F.69622 Villeurbanne, France.



**Figure 1** Skull, mandible and first molars of *Oenomys* Thomas 1904. (A) Skull and mandible of *Oenomys hypoxanthus* (Burundi, specimen GT 240–1993–2123, coll. MNHN, Paris). Scale bar 1 cm. (B) First upper and lower molars of *O. ornatus*, West Africa (Ivory Coast, specimen 422–1979, coll. MNHN, Paris). Scale bar 1 mm. (C) First upper and lower molars of *O. hypoxanthus*, Central Africa (Gaboon, specimen 1995–3029, coll. MNHN, Paris). Scale bar 1 mm. (D) First upper and lower molars of *O. hypoxanthus*, East Africa (Burundi, specimen GT 240–1993–2123, coll. MNHN, Paris). Scale bar 1 mm.



**Figure 2** Location of *Oenomys* samples across the tropical forest zone of Africa. Labels are the identifying numbers in Table 1.

the cusps in a garland-like dental pattern on the upper molar; this has been interpreted as an adaptation to a more abrasive diet, probably an adaptation to the herbivorous diet characteristic of this rodent (Dieterlen, 1967). Two modern

species have been recognized, based on morphological (Rosevear, 1969) and chromosomal data (Tranier & Gautun, 1979; Maddalena *et al.*, 1989): *O. ornatus* Thomas 1911, ranging across the west African forest block from Guinea to Ghana, is characterized by a small size and a bright fur colour; the rufous-nosed rat *O. hypoxanthus* (Pucheran 1855) is larger, clearer in colour and ranges across the tropical forest block from Nigeria to Uganda and Kenya (Wilson & Reeder, 1993). Except for size comparisons, no attempt has been made to establish an osteological differentiation between these extant species. The present study uses a Fourier transform method to quantify the differences in shape by analysing the two-dimensional outline of the upper and lower first molars, the only material available on both living and fossil samples. The geographical patterns of size and shape differentiation are established and the constraints and mechanisms which have led to these patterns are discussed.

## MATERIAL AND METHOD

### Material

The right and left first upper and lower molars of 198 skulls of *Oenomys* from forty localities (Fig. 2 and Table 1), housed in either the Museum National d'Histoire Naturelle, Paris, or the Natural History Museum, London, were measured. Where sample size was small (one or two skulls), the data were pooled on the basis of geographical proximity (Table 1). Two neighbouring localities from Burundi, Tora and Ntentamaza, with large sample sizes and individual statistics (e.g. sex and weight) provided background information on the expected

**Table 1** Localities composing the groups used in the study, with corresponding latitude and longitude. M1/(M/1): First upper molars (lower molars) sample size. RCA: Central African Republic.

No.	Group	Country	Locality	M1/	M/1	Lat.	Long.
1	GUI	Guinea	Seredou	22	22	3.31	-9.32
2	GUI	Guinea	Mts Nimba	1	1	7.39	-8.3
3	CIV	Ivory Coast	Lamto	5	5	6.33	-5.01
4	GHA	Ghana	Kumasi	4	4	6.45	-1.35
5	NIG	Nigeria	Umuaahia	2	2	5.31	7.26
6	CAM	Cameroun	Buea	1	1	4.09	9.1
6	CAM	Cameroun	Musake	1	1	4.13	9.1
7	CAM	Cameroun	Manehasq	1	1	4.51	9.46
8	CAM	Cameroun	Makak	2	2	3.32	11.05
9	CAM	Cameroun	Yaounde	2	2	3.51	11.31
10	YOK	Cameroun	Yokadouma	7	7	3.26	15.06
11	YOK	RCA	Lidjombo	1	1	2.32	16.03
12	RCA	RCA	La Maboke	16	13	3.53	18.01
13	RCA	RCA	Bangui	5	5	4.23	18.37
14	RCA	RCA	Botambi	1	1	4.09	18.31
15	RCA	RCA	Ippy	2	2	6.05	21.07
—	RCA	RCA	?	3	2	—	—
16	GAB	Gaboon	Lambarene	2	2	-0.41	10.13
17	CGO	Congo	Menengue	4	4	-4.16	11.48
18	CGO	Congo	Pointe Noire	1	1	-4.46	11.53
19	CGO	Congo	Kuilila	2	2	-4.3	12.3
20	CGO	Congo	Sibiti	1	1	-3.4	13.24
21	CGO	Congo	Brazzaville	2	2	-4.41	15.14
22	CGO	Congo	Djoumouna	1	1	-4.23	15.1
23	CGO	Congo	Kidamba	1	1	-3.48	14.32
24	CGO	Congo	MBila	2	2	-3.12	13.2
25	CGO	Congo	Dimonika	1	1	-4.14	12.25
—	CGO	Congo	?	1	1	—	—
26	ZAI	<i>ex-Zaire</i>	Kananga	1	1	-6.21	21.13
27	ZAI	<i>ex-Zaire</i>	Luluabourg	5	5	-5.53	22.26
28	ZAI	<i>ex-Zaire</i>	Inkongo	3	3	-4.55	23.15
29	BUR1	Burundi	Ntentamaza	28	28	-3.4	29
30	BUR2	Burundi	Tora	44	44	-3.42	29.33
31	UGA	<i>ex-Zaire</i>	Rutshuru	4	4	-1.11	29.28
32	UGA	Uganda	Kigeri	1	1	-1.15	30
33	UGA	Uganda	Bundi Mali	2	2	0.55	30.03
34	KEN	Uganda	Kampala	5	5	0.19	32.35
35	KEN	Kenya	Kaimosi	4	4	0	35
36	KEN	Kenya	Kangaita	1	1	-0.31	37.18
37	KEN	Kenya	Mt Kenya	1	1	-0.1	37.19
38	EAST	Kenya	Wajir	4	4	1.46	40.36
39	EAST	Ethiopie	Omo	1	1	7.28	37.28

within-and among-population variation of size and shape variables.

#### Fourier analysis of the outline

The outline, rather than landmarks, was chosen here as a descriptor of tooth morphology, since the location of the landmarks seemed more sensitive than the outline to modifications of the dental pattern occurring with wear, and the outline described effectively the location of the tubercles characteristic of the tooth morphology. Outlines, even complex ones, can be simply described using a Fourier analysis (Foote, 1989). This method is independent of the orientation of the

outline, limits the influence of error by filtering the background noise occurring in details of the outline and has been proven efficient in describing morphological differentiation in similar rodents (Renaud *et al.*, 1996).

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 sixty-four points equally spaced along the outline were extracted semiautomatically using an optical image analyser (OPTIMAS v.4.0), with each skull or mandible positioned so that the tooth row was horizontal. The starting point of the outline is defined as the maximum curvature at the fore-part of the tooth. From these coordinates, sixty-four radii are calculated, corresponding to the distance of each

of the points to the centroid of the sixty-four points defining the outline of the tooth. A discrete Fourier transform is then applied to this set of sixty-four radii; the outline is thus expressed as a finite sum of trigonometric functions of decreasing wave length, i.e. the harmonics, according to the formula:

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

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 coefficients  $a_n$  and  $b_n$  are calculated according to the formula using the complex numbers:

$$b_n = a_n + ib_n = \sqrt{\frac{1}{K} \sum_{s=1}^K r(s) e^{2\pi i(s-1)(n-1)/K}}, \quad (2)$$

where  $a_n$  is the real part and  $b_n$  the imaginary part of the complex Fourier coefficient  $b_n$ .

The size is then standardized by dividing all the coefficients by the zeroth harmonic amplitude,  $a_0$ , which is proportional to the diameter of a circle with the same area as the digitized outline, and can thus be used as a measure of size (Ehrlich & Weinberg, 1970). In order to buffer the asymmetry between right and left molars within each individual, left molars were subjected to a mirror image and measured as right molars. For each individual and each Fourier coefficient, the mean value of the right and left sides was considered to describe the mean tooth morphology.

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 in calculating the Fourier coefficients (Rohlf & Archie, 1984).

A characteristic of the Fourier harmonics is that the higher the rank 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 rank (Renaud *et al.*, 1996). Thus, the effect of noise was detected by expressing measurement error as a function of the harmonic rank. Measurement error was estimated by five repeated measurements of five specimens, and expressed as the mean coefficient of variation of the harmonic amplitude ( $= \sqrt{(a_n^2 + b_n^2)}$ ). Results indicated an increase in measurement error with the harmonic number as predicted (Fig. 3). The effect of measurement error was limited by considering only Fourier coefficients up to the ninth harmonic for the upper molars and up to the seventh for the lower molars. Above these threshold harmonics, the measurement error reached values greater than 25% of the signal, rendering the Fourier coefficients unreliable.

Note that the measurement error increased faster for the lower molar than for the upper molar. This is due to the fact that the outline of the lower molar is more roughly trapezoidal, and displays fewer 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 molar. In this case, the outline could not be reconstructed with the inverse Fourier transform.

### Analysis of the sex and age variability

Prior to the analysis of geographical differentiation, the main factors of within-group variability were tested. Using ANOVA (analysis of variance) on the size estimator and MANOVA (multivariate analysis of variance) on the Fourier coefficients, size and shape differences between neighbouring localities and sexual dimorphism were tested. The possible influence of differences in weight, a rough estimator of the age of the animals, was tested using a linear regression for the size, and a multiple regression model for the shape, the different variables being the Fourier coefficients.

### MANOVA on the Fourier coefficients

A set of eighteen Fourier coefficients for the each upper molar and of seven Fourier amplitudes for each lower molar was obtained. A MANOVA was performed on these variables in order to display the relationships among group means relatively to within-group variability. In this analysis, the groups correspond to recent trapping localities or a pooling of neighbouring localities. The MANOVA then effects a canonical variate analysis. 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 the variations in morphology and the relative position of the samples can be visualized.

Geographic variation in size of *Oenomys* was also tested in order to be compared to shape variation. As the zeroth harmonic amplitude  $a_0$  is proportional to the size of each tooth, it was selected as the size variable. Analysis of variance (ANOVA) was used to test the existence of among-localities size differences.

### Analysis of climatological data

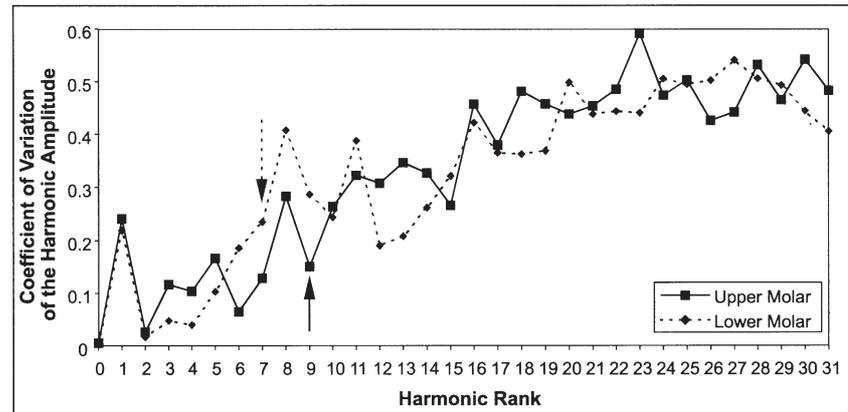
Mean climatic data were collected from a climatological Atlas of Africa (Jackson, 1961) in order to study the relationship between variation in climate and in size and shape. For each locality, the climatic data consisted in altitude, mean annual rainfall, mean monthly maximal and minimal rainfall, seasonal precipitation difference; mean annual temperature, mean monthly maximal and minimal temperature, mean diurnal maximal temperature, daily difference in temperature, mean annual humidity, and seasonal humidity difference. A PCA (principal component analysis) was performed on these data in order to obtain a few synthetic principal axes expressing most of the climatic variability.

## RESULTS

### Local size and shape variability

The existence of a size or shape difference of the molars due to local differentiation, sex or age of the individuals was first

**Figure 3** Measurement error as a function of the harmonic rank. Five specimens were measured five times; the measurement error is expressed as the mean coefficient of variation of the harmonic amplitude ( $=\sqrt{(a_n^2 + b_n^2)}$ ) of the five specimens. The arrows indicate the threshold rank for the upper molar (full line) and the lower molar (dashed line).



**Table 2** Tests of within-group variability. Locality: test of the differences between Tora and Ntentamaza. Sex: test of the differences between the sexes, Tora and Ntentamaza pooled together

Factor	Size				Shape				
	<i>F</i>	<i>P</i>		Wilk's $\lambda$	<i>df1</i>	<i>df2</i>	<i>P</i>		
Upper molar	Locality	1.19	0.28	ns	0.752	18	53	0.5	ns
	Sex	0.72	0.39	ns	0.688	18	48	0.29	ns
Lower molar	Locality	2.22	0.14	ns	0.905	7	64	0.47	ns
	Sex	0.48	0.49	ns	0.815	7	64	0.08	ns
		$r^2$	<i>P</i>				$r^2$	<i>P</i>	
Upper molar	Weight	0	0.65	ns			0.21	0.77	ns
Lower molar	Weight	0	0.88	ns			0	0.88	ns

tested on the two large samples of *O. hypoxanthus* from Burundi, Tora ( $N=28$ ) and Ntentamaza ( $N=44$ ).

The two neighbouring localities displayed no differentiation either in size or shape (Table 2), so the samples were pooled for further analyses of within-group variability. No sexual dimorphism was found on the molars for either size or shape (Table 2). Furthermore, no correlation of either size or shape with weight, a rough indicator of the age of the animals, was significant (Table 2). Therefore, the molar outline was not affected by wear. All teeth from one locality could thus be pooled into a single group. The absence of local differentiation also justified the grouping of neighbouring localities with small sample sizes into larger geographical groups.

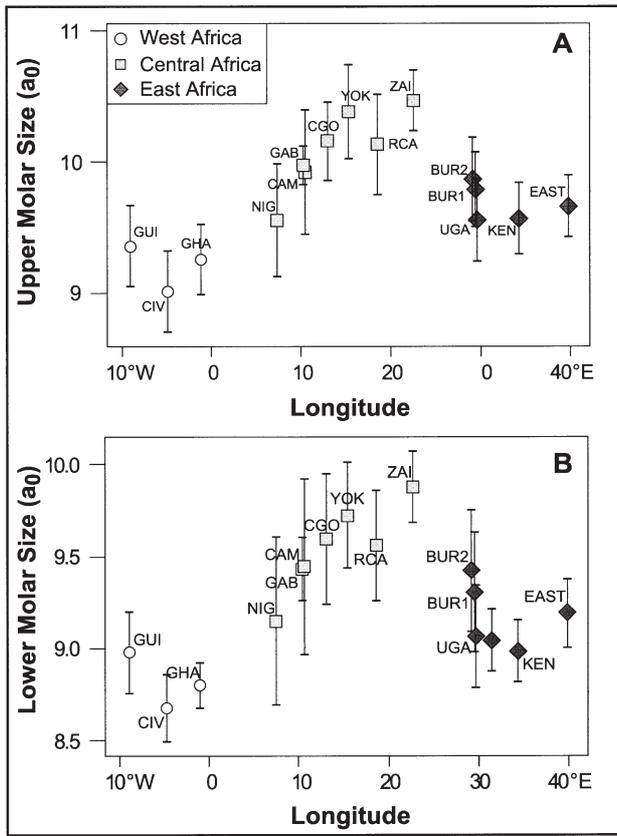
### Geographic size variations

According to the previous analyses, the main source of variation was expected to be geographical. The size of upper (Fig. 4A) and lower (Fig. 4B) molars were highly correlated with each other ( $r^2=0.978$ ,  $P<0.001^{***}$ ) and both displayed strong longitudinal variations across Africa. The samples from West Africa were characterized by a small size. This was in accordance with the smaller body and head size of *Oenomys ornatus* (Rosevear, 1969). More surprisingly, a strong size

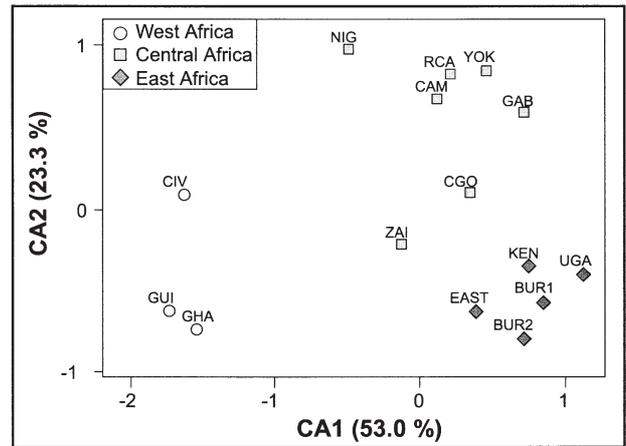
differentiation existed within the geographical range of *O. hypoxanthus*. A separation between small Eastern and large Central African molars was obvious and located around Lake Tanganyika. A trend within the Central African *Oenomys* exists from relatively small molars in Nigeria to the largest molars in Zaire and the Central African Republic.

### Geographic shape variations

The MANOVA on the Fourier coefficients of the first upper molar indicated that a morphological differentiation was present among the groups of *Oenomys* (Wilk's Lambda=0.061, *degree of freedom1*=252, *df2*=1890.4,  $P<0.001^{***}$ ). Globally, the morphological distances between the groups in the canonical space (Fig. 5) were strongly correlated to the geographical distances between groups (Mantel *t*-test:  $r=0.660$ ,  $t=5.689$ ,  $P<0.001^{***}$ ). As for size, the samples from West Africa corresponding to *O. ornatus* appeared strongly differentiated from the other samples. This supported the identification of the West African *Oenomys* as a valid species distinguished in part by molar size and shape. Furthermore, the samples from Central and East Africa seemed to segregate along the first canonical axis. This, as well as the pattern of size differentiation, suggested the existence of two different species or subspecies



**Figure 4** Mean size  $\pm$  standard deviation of the different groups plotted against longitude. Size is estimated by the zeroth harmonic amplitude  $a_0$ . (A) Upper molar. (B) Lower molar. Labels correspond to the group code (Table 1).

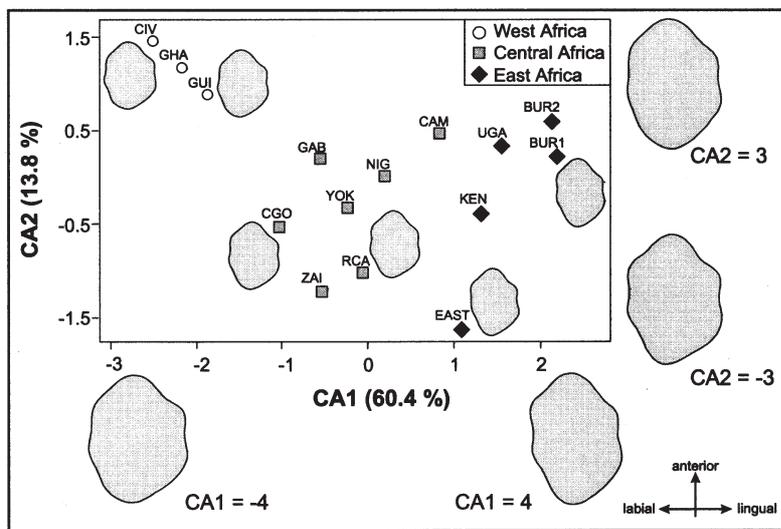


**Figure 6** First two canonical axes for the lower molar.

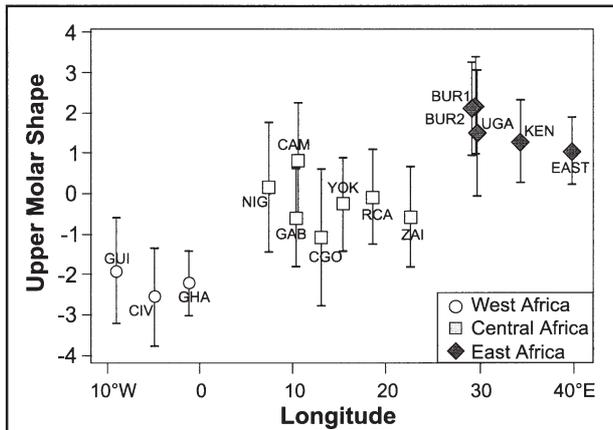
corresponding to Central Africa and East Africa, although no chromosomal differences seemed to exist between them (Maddalena *et al.*, 1989).

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 showed the differences involved in this geographical shape differentiation. The first canonical axis corresponded to a longitudinal shape gradient opposing the symmetrical outlines of the West African samples to the asymmetrical and constricted outlines from East Africa, the Central African samples being intermediate. Central and East African groups were further characterized by a less pronounced posterior labial tubercle still present in the western *O. ornatulus*.

A MANOVA performed on the Fourier amplitudes of the lower molar (Fig. 6) also indicated a morphological differentiation (Wilk's Lambda=0.271,  $df_1=35$ ,  $df_2=734.4$ ,  $P < 0.001^{***}$ ).



**Figure 5** First two canonical axes and corresponding outlines for the upper molar. 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.



**Figure 7** Mean upper molar shape  $\pm$  standard deviation of the different groups plotted against longitude. Shape is estimated by the coordinates along the first canonical axes (CA1).

The pattern of shape differentiation of the lower molar was strongly correlated to that of the upper molar (Mantel  $t$ -test:  $r=0.605$ ,  $t=4.430$ ,  $P < 0.001^{***}$ ). The first canonical axis distinguished the West African samples from the other groups, and the Central and East African samples were divided along the second canonical axis. This result further supported the existence of three groups of *Oenomys*, possibly corresponding to three species. The West African group, corresponding to *O. ornatus*, is the smallest and morphologically the most distinct; the East African group is relatively small and is morphologically characterized by a constricted outline of the upper molar and a pinched rear; finally, the Central African group is characterized by the largest size but a morphology intermediate between that of the West and East African groups.

## DISCUSSION

### Different patterns of size and shape differentiation

Three morphological groups of *Oenomys* emerge from the present analysis. However, the patterns of size and shape differentiation among them seem to be different. For both size and shape, the West African group corresponding to *O. ornatus* is the most divergent. The importance of the shape differentiation between the Central and Eastern African groups is, however, of the same order of magnitude, and the mean shape of each group can be characterized without any important within-group variation with longitude (Fig. 7), suggesting a genetic isolation between these populations. However, size is globally different between the Central and Eastern *Oenomys* but displays strong longitudinal variation within each group, especially within the Central African one (Fig. 4).

### Size variations related with climatic gradients

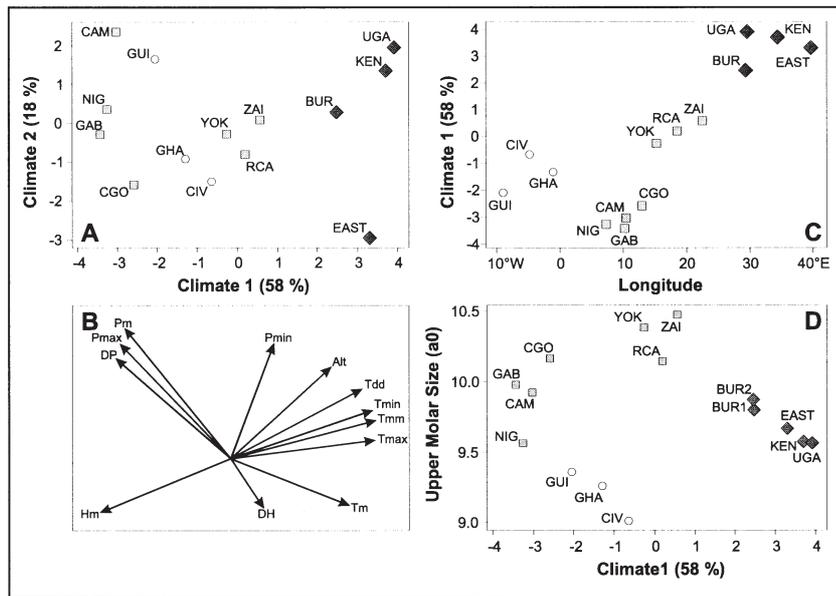
In order to understand the significance of these size variations a relation with climatic gradients was evaluated. Accurate

climatic data were not available for the different localities, so no detailed study was possible. However, mean climatic data collected from a climatological Atlas of Africa (Jackson, 1961) allowed us to perform a large-scale analysis of climatic differences among the localities using a principal component analysis (Fig. 8A). The first axis of this analysis explained most of the climatic variability among localities (58%) and corresponded to a gradient of decreasing humidity and increasing temperature correlated with altitudinal variations (Fig. 8B), while the second climatic axis (18% of the variance) mostly represented a trend of increasing rainfall. This analysis showed that eastern localities were characterized by warm and dry conditions. The western localities could not be distinguished from the Central African ones on a climatic basis, but a climatic gradient was identified within the Central African localities, corresponding to decreasing humidity and increasing temperature eastwards (Fig. 8C).

When compared to size variations, these climatic gradients appeared to be related to size trends in the three groups of *Oenomys* (Fig. 8D), but no global trend for the whole genus was evident (regression between the group means:  $r^2=0.02$ ,  $P=0.860$  ns). This was due to the fact that the western and eastern groups exhibited a relationship to climate inverse of that of the Central African group. For the western and eastern groups of *Oenomys*, size seemed to be negatively related to the climatic axis of increasing temperature and decreasing aridity, whereas it significantly increased within the Central African group (regression between the group means:  $r^2=0.62$ ,  $P=0.035^*$ ). The important size variability within the Central group of *Oenomys* was therefore due to a strong influence of a climatic gradient on size in this group. On the contrary, no significant variation of the shape could be detected along this climatic gradient (regression between the group means of the Central African groups:  $r^2=0.03$ ,  $P=0.688$  ns). A significant relationship between shape and climate was, however, observed for the whole genus ( $r^2=0.39$ ,  $P=0.013^*$ ), but could be ascribed to the step-like shape change from the Western to the Eastern group.

### Different evolutionary control on size and shape

The different reactions of size to climatic variations (Fig. 8D) further supported the hypothesis of a genetic differentiation between the three morphological groups of *Oenomys*. The three groups would thus be characterized by a typical shape and mean size as well as by a particular relationship between size and environment. This discrepancy between size and shape can be due to different evolutionary mechanisms. Size is known to be a character with multigenic determinism and to vary with a wide range of environmental factors (Nevo, 1989) while shape seems to more strongly under the genetic control of a few developmental genes (Whiting & Wheeler, 1994). Such a discrepancy between the constraints and determinisms acting on size and shape can lead to different evolutionary patterns, and a gradual evolution of size combined with a nonprogressive evolution of shape has been recorded in Plio-Pleistocene fossil rodents exhibiting a morphological convergence with the dental pattern of *Oenomys* (Renaud *et al.*, 1996). The implications of



**Figure 8** Relation between climatic and biogeographic variations. (A) First principal plane of a PCA on twelve climatic variables estimated for each group. (B) Participation of each climatic variables to the first two principal axes. (C) Climatic variations along longitude. (D) Variation of the upper molar size with climate. Climatic variables are:  $Alt$ , altitude;  $P_m$ , mean annual rainfall;  $P_{max}$ , mean monthly maximal rainfall;  $P_{min}$ , mean monthly minimal rainfall;  $DP$ , seasonal precipitation difference;  $T_m$ , mean annual temperature;  $T_{max}$ , mean monthly maximal temperature;  $T_{min}$ , mean monthly minimal temperature;  $T_{minn}$ , mean diurnal maximal temperature;  $T_{dd}$ , mean daily difference in temperature;  $H_m$ , mean annual humidity;  $DH$ , seasonal humidity difference.

such results on biogeographical studies are that shape is most susceptible to display phylogenetic information while size can be more sensitive to environmental variations.

### Timing of the differentiation events

The present study has shown a pattern of geographical differentiation of *Oenomys* more complex than previously thought, corresponding to three genetically isolated populations. The dating of these differentiation events is, however, difficult and only speculations can be proposed.

The western group, corresponding to *O. ornatus*, is the most divergent one, both in size and shape. It is further characterized by a particular chromosomal number (Tranier & Gautun, 1979; Maddalena *et al.*, 1989) and it can be assumed that this group diverged first from the ancestral pool. This group is limited to the West African forest block, which is characterized by a strong faunal differentiation from the main African forest block. This disjunction is attributed to the Dahomey Gap, a zone of lower rainfall between the Volta and the Niger rivers which separates the central part of the western forests (Booth, 1954). This arid gap may be as old as 3 Ma, since sedimentological evidence shows an increase in aridity and dust supply off West Africa at this time (Robert & Chamley, 1987). Molecular analyses have estimated the time of cladogenesis between *Oenomys* and *Arvicanthis* at about 5 Ma (Chevret *et al.*, 1993) and the divergence of *O. ornatus* may thus have occurred relatively early in the history of the genus.

The Central and Eastern African groups are morphologically less differentiated and would have diverged later. Their extant distribution can be related to different habitats, the Central African group inhabiting lowland forest while the East African group is characteristic of montane forests, and their morphological and genetic divergence may have occurred

following a segregation by the habitat. The existence of montane forests in tropical Africa is linked to the East African rift system which is older than 30 Ma (Denys *et al.*, 1985). The ecological differentiation may therefore be an ancient feature and the genetic divergence of the two populations would have occurred progressively. This divergence may have been enhanced by the successive fragmentation of the rain forest caused by the climatic oscillations during the Quaternary (Maley, 1996), during which both habitats still existed but were no longer in contact. During the arid phases, mountain forests expanded to lower altitudes but the lowland forest habitat was still present as riparian forests corresponding to a 'major fluvial refuge' (Colyn *et al.*, 1991).

If such hypotheses are correct, the divergence between the three morphological groups of *Oenomys* would be ancient and should thus correspond to a noticeable genetic divergence. Only molecular analyses of the three groups of *Oenomys* would allow to test these hypotheses.

### CONCLUSION

A morphometric study of the African rodent genus *Oenomys* has shown the existence of a size and shape differentiation between the two known species, and furthermore indicates the existence of two potential cryptic species, unidentified using traditional approaches. This result shows that speciation events can be detected using morphometric approaches, an encouraging fact for the application of these methods to similar but entirely fossil material (Renaud *et al.*, 1996), where the concept of fossil species is used by default without modern references. If shape variations are mostly dependent on phylogeny, size displays important variations within each groups related to climatic gradients and therefore appears to bear less reliable phylogenetic information. Such a discrepancy may be linked to different genetic determinisms and constraints

underlying the evolution of both characters. The dating of the divergence events between the three morphological groups remains speculative. However, the amplitude of the morphological divergence as well as environmental data suggest that the Western African group, corresponding to *O. ornatus*, may have diverged first and perhaps has early as 3 Ma ago. The divergence between the Central and the Eastern group of *O. hypoxanthus* could be related to different ecological preferences and would have occurred during the Plio-Pleistocene climatic fluctuations. Testing these phylogenetic hypotheses, however, requires further molecular analyses of the genus.

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## BIOSKETCH

Sabrina Renaud received her Doctorat from the University of Montpellier II in 1997 working on the quantification of morphological evolutionary patterns in murine rodents. After an EU postdoc at ETH, Zurich on evolution and biodiversity of coccolithophores (CODENET project), she is now pursuing her research at the CNRS, Centre de Paléontologie Stratigraphique et Paléocéologie, Université Lyon 1. Her research interests focus on the use of morphometrical methods for quantifying evolutionary patterns on various types of organisms, and the use of such quantitative tools for better understanding the constraints and determinants of the morphological evolution.