

## Morphological evolution of the murine rodent *Paraethomys* in response to climatic variations (Mio-Pleistocene of North Africa)

Sabrina Renaud, Mouloud Benammi, and Jean-Jacques Jaeger

**Abstract.**—The North African murine rodent *Paraethomys* evolved as an anagenetic lineage from the late Miocene until its extinction in the late–middle Pleistocene. A Fourier analysis of the outlines of the first upper and lower molars of this rodent was used to quantify the evolutionary patterns of this lineage and to compare evolutionary patterns to the climatic record. Morphological evolution and long-term environmental variations are strongly correlated. A change in molar shape, which may be related to the development of a more grass-eating diet, corresponds to the global cooling beginning around 3 Ma and the subsequent increase in aridity in North Africa. Concurrently, size increased, which may be related to increased masticatory efficiency or to metabolic adaptation to the cooler environmental conditions according to Bergmann's rule. This adaptive response to changing environmental conditions corresponds to an acceleration of evolutionary rates in the lineage. The modalities of the evolutionary response in size and shape are probably controlled by intrinsic factors such as different genetic determinisms for both characters.

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### Introduction

Patterns and rates of evolution, as estimated from the fossil record, have been widely discussed in the paleontological literature, since their interpretation provides insight into the underlying mechanisms of evolution. Beyond the debate between punctuated equilibria and phyletic gradualism, recent attempts have been made to distinguish passive trends from active ones, where evolution appears to be directional and can be supposed to be driven by selection (McShea 1994; Wagner 1996). Studies based on observed evolutionary patterns allow us to identify possible factors driving morphological evolution. Of these possible factors, one of the most likely for long-term evolution is the influence of changing environments. Although this influence on rate and direction of evolution has not been stressed in major evolutionary theories (Gingerich 1984; Gould and Eldredge 1977, 1993), recent models propose that environmental variations may influence evolutionary patterns to a significant degree (Vrba 1992, 1995; Sheldon 1993, 1996).

This study quantifies the morphological evolution of a North African murine rodent,

*Paraethomys*, in order to compare evolutionary and climatic records and to examine the hypothesis of an important climatic influence on morphological evolution. From the late Miocene until its extinction in the late–middle Pleistocene, *Paraethomys* was a dominant component of the North African murine rodent fauna. During this period, *Paraethomys* evolved as a single anagenetic lineage (Jaeger 1977) with an increase in size and the progressive development of a specialized dental pattern (Jaeger et al. 1975). The first stages of this evolutionary trend are characterized by a primitive murine dental pattern (Fig. 1A) probably associated with an omnivorous-granivorous diet. *Paraethomys* later developed a special dental pattern (Fig. 1B) named “stephanodonty” (Schaub 1938; Misonne 1969). Because *Paraethomys* has no living relatives, direct comparison for interpreting the adaptive significance of this dental specialization is impossible. However, stephanodonty can be interpreted as an adaptation to grass-eating by analogy with the extant African stephanodont murines *Oenomys* (Dieterlein 1967) and *Aethomys* (Denys 1994).

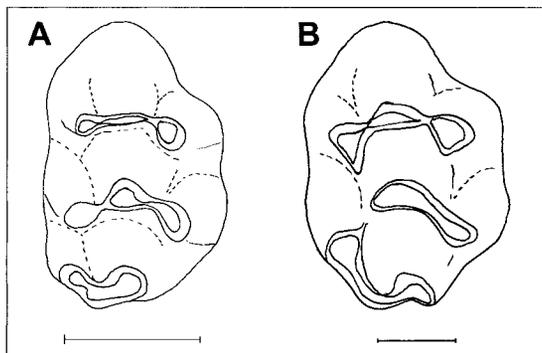


FIGURE 1. First upper molars of *Paraethomys*. A, Example from Wanou (7.8 Ma), exemplifying a primitive dental pattern. B, Example from Irhoud DV (1.0 Ma), showing more derived morphology. Scale bars, 1 mm.

Evolutionary trends in *Paraethomys* correlate well with environmental conditions in North Africa during this period. Since the late Miocene, the West African margin is characterized by an increase of eolian quartz in marine sediments (Diester-Haas and Chamley 1978; Robert and Chamley 1987), corresponding to the development of desert conditions in the Sahara. Ctenodactylidae are components of the North African faunas (Jaeger 1977). Their living relatives are characteristic of arid and semi-arid habitats and suggest that climatic differentiation of the North African region may have developed as early as the late Miocene. *Paraethomys* would thus have evolved in a rather arid environment, usually interpreted as being unfavorable to murine rodents. Arid conditions suggest that during the Mio-Pliocene, North African small mammals were subjected to isolation leading to endemism (Geeraards 1998).

A number of deposits (well dated using magnetostratigraphy, radiometric chronologies, and biostratigraphy) were available for this study. The good chronological framework allows both reliable estimates of evolutionary rates along the *Paraethomys* lineage and comparison of the continental evolution of *Paraethomys* with marine climatic records. Size and shape of first upper and lower molars, which are the most abundant and most characteristic fossils of murine rodents, have been quantified using an outline analysis based on Fourier transform. The evolutionary patterns characterizing the *Paraethomys* lineage have been

analyzed, as well as the rate of morphological evolution. The results of these analyses have been compared with the marine climatic record in order to clearly assess the relationship between evolution and environmental variations and to understand the modalities of the response of organisms to environmental variations. Finally, the results are used to examine existing models of interactions between evolution and the environment.

### Geological and Chronological Setting

The deposits used in this study are located in Morocco and Algeria (Fig. 2A), and most of them are of lacustrine or karstic continental origin. In a few cases, however, marine intercalations in the formation enclosing the small mammals allowed correlation of the continental biostratigraphy with the marine domain (Fig. 3).

*Aït Kandoula Basin (Morocco).*—The Aït Kandoula Basin is located on the southern slope of the Haut-Atlas (Fig. 2B). It covers approximately 330 km<sup>2</sup> and its continental basin-fill is mostly the product of erosion of the nearby uplands. The continental formations accumulated in the Liassic dolomite syncline of the Toundout nappe (Laville 1975; Fraissinet 1989). In the western part of the basin, fluvio-lacustrine deposits consisting mainly of conglomerates formed during synorogenic activity. In the central part, an alternation of limestone, clay, and ash, showing no visible discontinuity, is attributed to lacustrine or palustrine sedimentation. This sedimentation corresponds to a period of low tectonic activity (Benammi et al. 1995, 1996).

The age of the micromammal faunas discovered in the Neogene continental formation of the Aït Kandoula Basin extends from the middle Miocene to the late Pliocene (Benammi et al. 1995). The stratigraphy of the Afoud section was determined using biostratigraphy, radiometric dating, and magnetostratigraphy (Benammi et al. 1996). In this continuous sedimentary succession, the presence of fossiliferous localities, the existence of an <sup>40</sup>Ar/<sup>39</sup>Ar-dated ash level (5.9 ± 0.5 Ma [Benammi et al. 1995]), and correlation with the geomagnetic polarity timescale of Cande and Kent (1995) (bottom of the section with

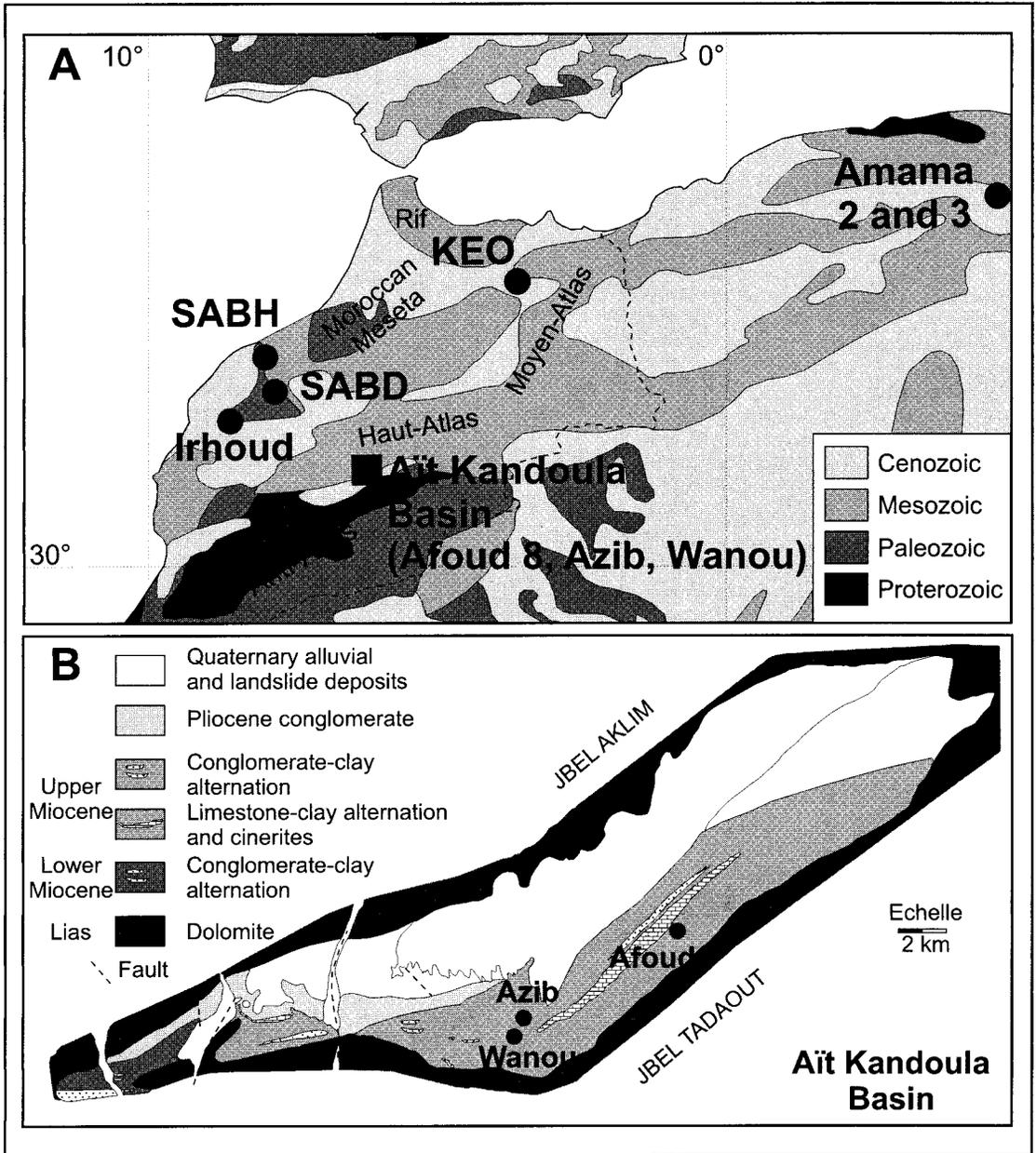


FIGURE 2. Location of fossil-mammal-bearing localities used in this study. A, General geological setting of the North African region (after Seber et al. 1997). B, Aït Kandoula basin with main geological features and location of the fossiliferous deposits considered in this study (after Benammi et al. 1996).

Chron C5n to the top of the section with Chron C3r) provide an estimated age of 5.23 Ma for the layer Afoud 8 (Benammi et al. 1996). The ages of the deposits of Wanou and Azib have been estimated by comparing their faunal composition of large mammals, *Cricetidae*, and *Muridae* with the faunal com-

position of the deposits dated using magnetostratigraphy and radiometric techniques (Benammi et al. 1995).

*Khendek-el-Ouaich (Morocco).*—This deposit is located in a lignite formation, characterized by the alternation of lagoonal and lacustrine levels, and is bracketed between marine and

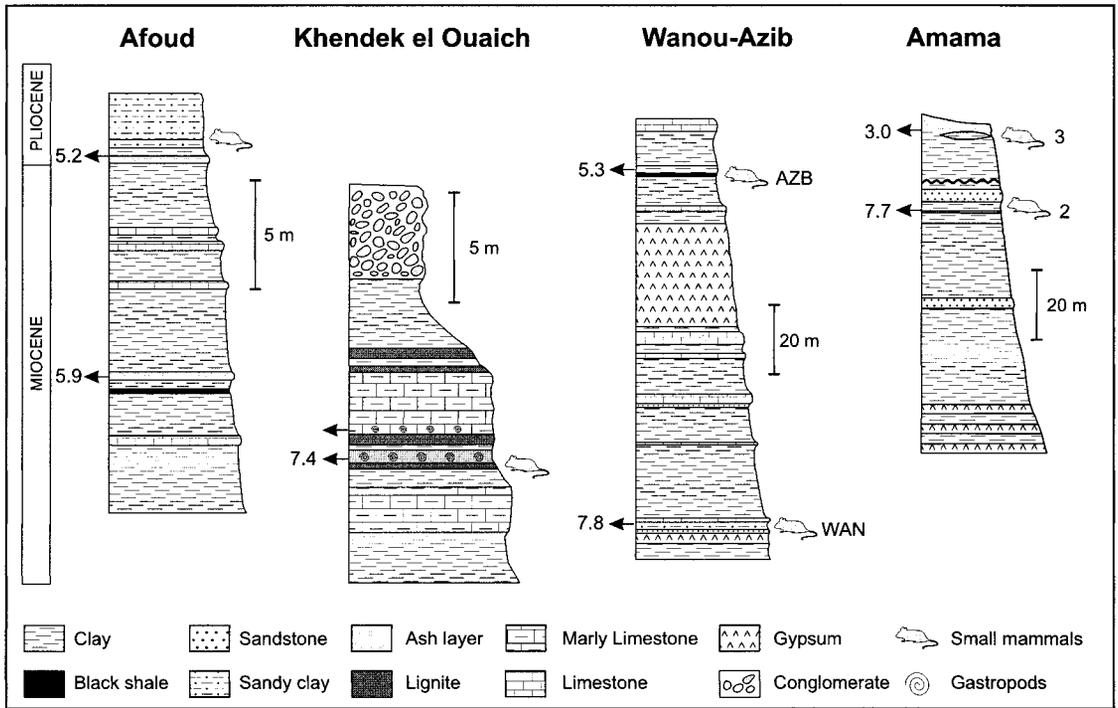


FIGURE 3. Lithology logs of the stratified deposits containing small-mammal fossils.

lagoonal formations (Fig. 3) that allow correlation of the continental fauna of the fossiliferous deposit with the marine Messinian faunas (Jaeger 1977). Furthermore, an ash layer has been recognized just above the fossiliferous level. It has been attributed to the activity of the Guilliz volcano and dated at 7.4 Ma (Choubert et al. 1968), thus allowing indirect estimation of the age of the small-mammal fauna (Jaeger 1977).

*Amama (Algeria).*—The continental formation containing the deposits of Amama (Fig. 3) starts with thick gypsum deposits progressively changing to bluish lacustrine clay enclosing several sandstone levels. These deposits are discordantly overlain by a formation of alluvial red clay containing a rodent fauna from a clay lens at its base (Jaeger 1977). Late Pliocene age of the mammal-bearing levels has been estimated through radiogenic dating of an intercalated ash layer below the site of Amama 2 (Coiffait 1991).

*Jebel Irhoud (Morocco).*—The Jebel Irhoud is a limestone block with archaeocyathids included in a Cambrian schist formation. New outcrops due to quarries allowed the discovery of

fossiliferous filling within recent solution caves, including the deposits of Irhoud Derbala Virage (IDV) and Irhoud Neanderthal. Their ages have been estimated at 1.0 and 0.6 Ma, respectively, by biostratigraphy using their small mammal fauna composed of Muridae, Arvicolidae, and Gerbillidae (Jaeger 1970).

*Sidi Abdallah.*—This locality is a cave-filling within a Devonian limestone. The filling, of approximately 2 m, is composed, at its base, of very fine pink clay that becomes hardened at the top. Micromammals were discovered within this latter facies (Jaeger 1977). This locality was attributed to the early Pleistocene according to its micromammal faunal composition of Sciuridae, Ctenodactylidae, Cricetidae, and Muridae.

*Sidi Abderahmane.*—This fossil-mammal-bearing locality southwest of Casablanca is in an abandoned quarry of Cambrian arkose. Fossiliferous exposures occur on a surface of approximately 15 ha (Biberson and Jodot 1962) and contain archaeological remains associated with a small mammal fauna. The age of the fauna, based on the presence of Crice-

TABLE 1. Age and sample size for the upper molars (U.M.) and lower molars (L.M.) of the different deposits.

Deposit	Code	Age	Species	U.M.	L.M.
Wanou	WAN	7.8	cf. <i>miocaenicus</i>	4	3
Khendek el Ouaich	KEO	7.7	<i>miocaenicus</i>	3	6
Amama 2	AMA2	7.6	<i>miocaenicus</i>	1	0
Azib	AZB	5.3	<i>pusillus</i>	5	2
Afoud 8	AF8	5.2	sp.	2	0
Amama 3	AMA3	2.9	<i>anomalous</i>	7	5
Sidi Abdallah 1	SABH	1.5	<i>rbiae</i>	1	7
Irhoud DV	IDV	1.0	<i>darelbeidae</i>	30	30
Sidi Abderahmane 2	SABD	0.9	<i>darelbeidae</i>	1	0
Irhoud Neanderthal	IRHN	0.6	<i>filfilae</i>	13	27

tidae, Gerbillinae, Arvicolidae, Gliridae, and Muridae, is late Pleistocene (Jaeger 1977).

### Materials and Methods

*Material.*—Sixty-seven first upper and 80 lower molars of several species of *Paraethomys* from ten North African localities (Fig. 2A) were measured. Their ages range from approximately 8 to 0.5 Ma, a range that samples the whole evolutionary history of the *Paraethomys* lineage. In all localities, only one species of *Paraethomys* was present. For composition, sample size, and age of each locality, see Table 1.

*Fourier Analysis of the Outline.*—The outline, rather than landmarks, was chosen here as a descriptor of tooth morphology since the location of landmarks seemed more sensitive than the outline to modifications of the dental pattern due to wear. In addition, the outline described effectively the location of the cusps characteristic of the tooth morphology. Even complex outlines can be simply described using a Fourier analysis (Foote 1989; Renaud 1999). This method is independent of the orientation of the outline, it limits the influence of error by filtering the background noise occurring in details of the outline, and it has been proven efficient in describing morphological differentiation and evolution in similar rodents (Renaud et al. 1996; Renaud 1997, 1999).

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 semiautomatically using an optical image analyzer (OPTIMAS v. 4.0). The starting point of the outline was defined as the maximum of curvature on the

forepart 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 discrete 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

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

where  $r$  is the radius at the abscissa  $s$  along the outline,  $L$  is the perimeter,  $K$  is the number of points along the outline, and  $n$  is the rank of the harmonic. The coefficients  $a_n$  and  $b_n$  are calculated according to the formula using the complex numbers

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

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

To get coefficients dependent only on shape, the size is standardized by dividing all Fourier coefficients by the zeroth harmonic,  $a_0$ , which is proportional to the diameter of the best-fit circle to the digitized outline and can thus be considered 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 detail of

the outline it describes. This property can be used to filter measurement error, which is expected to increase with the harmonic rank (Renaud et al. 1996). A study of the measurement error as a function of the harmonic rank on similar material (Renaud 1999) estimates the measurement error as the mean coefficient of variation of the harmonic amplitude ( $= \sqrt{a_n^2 + b_n^2}$ ) for five repeated measurements on five specimens. This study indicates that the effect of measurement error can be limited by considering only Fourier coefficients up to the ninth harmonic for the upper molars and up to the sixth for the lower molars. Above these threshold harmonics, the measurement error reached values greater than 20% of the signal, rendering Fourier coefficients unreliable. Since the definition of the starting point is less accurate on the lower than on the upper molars, only the harmonic amplitudes that are independent of the starting point are used for the morphometric analysis of the lower molars. In this case, the outline can not be reconstructed with the inverse Fourier transform.

*Multivariate Analysis of the Fourier Coefficients.*—For each tooth, 18 coefficients for upper molars and 6 amplitudes for lower molars were obtained. A principal component analysis (PCA) was performed on these coefficients to display the morphological variability on a few synthetic principal axes. The PCA was normed, i.e., performed on the correlation matrix of the coefficients, to give the same weight to all the variables and not to enhance the rule of the first harmonics because of their higher numeric values.

#### Patterns of Morphological Differentiation

The PCA on the Fourier coefficients of the first upper molars (Fig. 4) indicates a clear differentiation between two morphological groups along the first principal component, PC1 (30% of the total variance) without any overlap between them. These two groups correspond to the Mio-Pliocene *Paraethomys* and

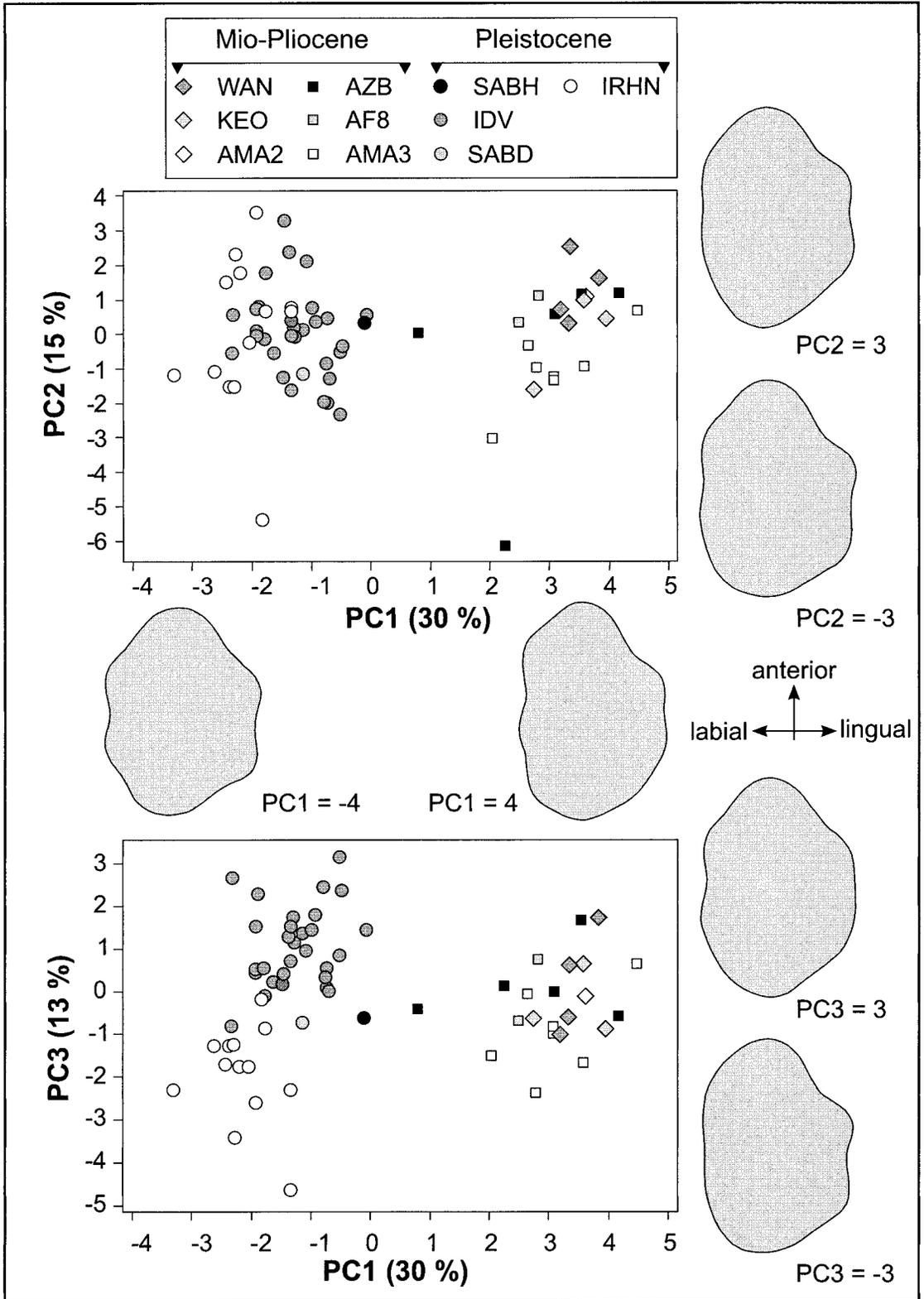
the Pleistocene *Paraethomys*. The pattern of shape differentiation along PC2 seems to correspond to a within-group variability exhibited in the Pleistocene *Paraethomys* groups IRHN and IDV as well as in the Pliocene *Paraethomys* sample from AZB. The variation along PC3 (13% of the variance) seems to correspond to a differentiation within the Pleistocene *Paraethomys*, with a clear segregation between IDV and IRHN, and within the Mio-Pliocene group to a possible differentiation of the *Paraethomys* of AMA3 from the Miocene samples.

The reconstruction of theoretical outlines corresponding to the principal axes allows us to visualize the morphological changes along the axes. The positive values of PC1 corresponding to the Mio-Pliocene rodents are characterized by an elongated and asymmetric outline (PC1 = 4 on Fig. 4). It is opposed to a more symmetrical outline with a more prominent posterior cusp and a labial anterior cusp displaced backward in the Pleistocene rodents (PC1 = -4 on Fig. 4). The second principal axis opposes tooth outlines with a flat rear (PC2 = -3 on Fig. 4) to outlines with a pinched rear (PC2 = 3 on Fig. 4). PC3 characterizes differences in the labial anterior zone. The labial anterior cusp is positioned more anteriorly and the labial cusps are less marked on the outline for the negative values of PC3 (PC3 = -3 on Fig. 4).

The PCA on Fourier coefficients of the lower molars (Fig. 5) exhibits a less clear pattern of differentiation. The first principal component PC1 (30% of the variance) segregates the Pleistocene *Paraethomys* from the Mio-Pliocene group, while PC2 seems to separate the Pleistocene samples from IRHN and IDV. No clear pattern emerges from PC3 (not represented here), which corresponds to within-group variability present in all groups. The lower molar appears to provide a pattern of morphological differentiation similar to that of the first upper molar, but with fewer details than

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FIGURE 4. First two principal planes and corresponding outlines of the PCA performed on Fourier coefficients of the upper molars. Opposed along the first principal axis PC1 are the Mio-Pliocene (squares and diamonds) and Pleistocene (circles) outlines. The reconstructed outlines are obtained using inverse Fourier transform on sets of coordinates along the canonical vectors.



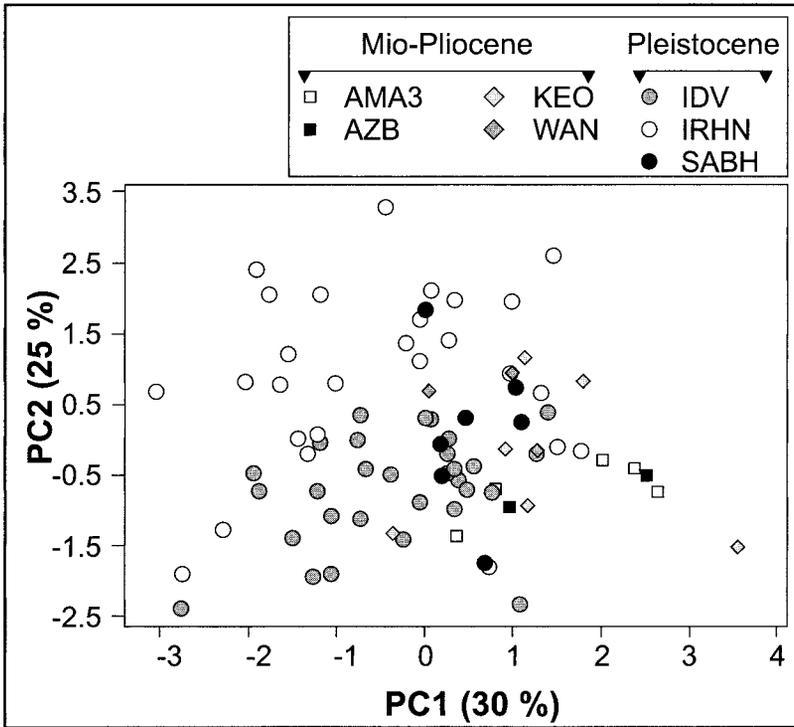


FIGURE 5. First principal plane of the PCA performed on Fourier amplitudes of the lower molars.

the upper molar. Similar results have been shown by other studies (Renaud 1997, 1999), perhaps because the lower molars display fewer characteristic morphological features than the upper molars.

**Evolution in Size and Shape**

The Fourier analysis of the molar outline indicates an important shape differentiation between Mio-Pliocene and Pleistocene rodents. Since the *Paraethomys* lineage has been interpreted as an example of anagenetic evolution based on size increase, it is important to estimate size evolution and compare the resulting pattern with shape evolution. For this purpose, we concentrate only on upper molars, which provide the clearest results. The zeroth harmonic  $a_0$  was selected to represent size and the first principal axis of the PCA on the Fourier coefficients of the upper molars was used to quantify shape.

The evolution of upper molar size (Fig. 6A) is characterized by a slight size increase during the Mio-Pliocene, followed by a large size increase between the samples from AMA3

(2.9 Ma) and SABH (1.5 Ma). During the Pleistocene, size increases only slightly. This size evolution is strongly related to shape evolution ( $r^2 = 0.906, p < 0.001$ ). The Mio-Pliocene period is characterized by a shape stasis. After AMA3, shape shows more evolution leading to the highly differentiated Pleistocene *Paraethomys* (Fig. 6B). The morphological evolution triggered between AMA3 and SABH continues during the Pleistocene, leading to the youngest and most derived sample of IRHN. For both size and shape the evolutionary pattern seems to have varied along the lineage, with a strong acceleration of the trend after AMA3 (2.9 Ma). This result appears robust with respect to the accuracy of dating of the different deposits. Only the exact timing of the acceleration of the evolution would be affected by a revision of the ages of the deposits.

**Relationship between the Evolution of *Paraethomys* and the Climatic Context**

Important climatic variations that characterize the Plio-Pleistocene of North Africa allow us to test for climatic influence on the evolu-

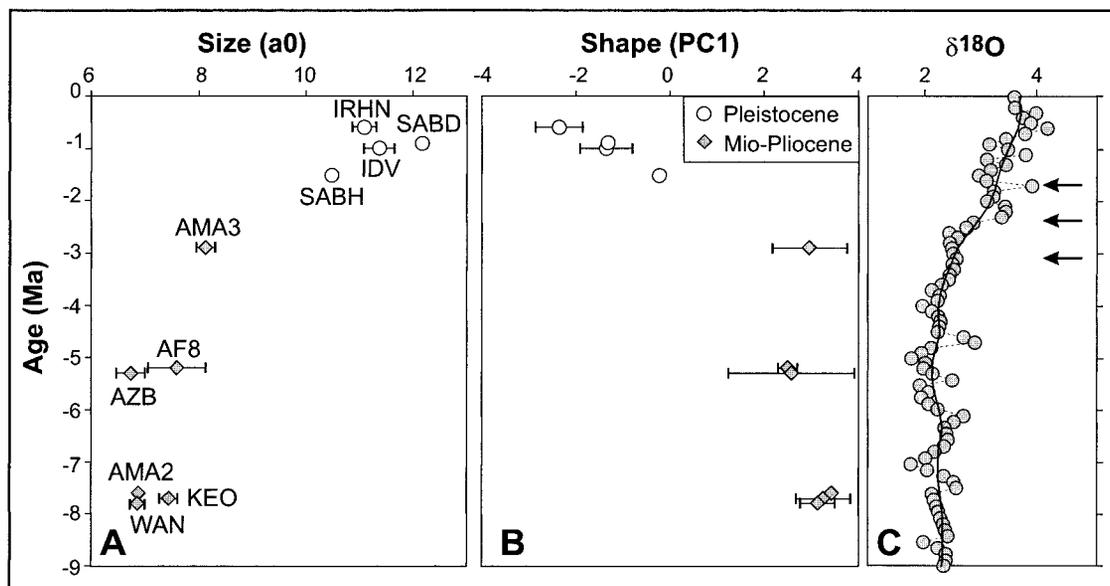


FIGURE 6. Evolutionary patterns of size and shape of upper molars of *Paraethomys*, compared with climatic record. A, Evolution of size, estimated by the zeroth harmonic  $a_0$ . B, Evolution of shape, estimated by coordinates along the first principal axis PC1. C, Climatic record, represented by a synthetic  $\delta^{18}\text{O}$  curve from Atlantic benthic foraminifers (after Miller et al. 1987). Arrows correspond to major cooling episodes.

tion of *Paraethomys*. Isotopic data are available for the Western Mediterranean (Vergnaud-Grazzini et al. 1990; Thunell et al. 1991), but these data do not cover the whole period of the *Paraethomys* lineage. Furthermore, the geographic location of *Paraethomys* localities (Fig. 1A) shows that most of them should be under Atlantic rather than Mediterranean climatic influence. We therefore selected a compiled  $\delta^{18}\text{O}$  curve from Atlantic benthic foraminifers (Miller et al. 1987) to compare with the evolutionary record of *Paraethomys* (Fig. 6C). Raw data were available as well as a smoothed curve obtained by Gaussian convolution filters removing frequencies higher than about 1 million years (Miller et al. 1987). The smoothed curve seemed more appropriate to use for the comparison since the correlation with the smoothed curve was less sensitive to uncertainties about the ages of the deposits bearing small mammals.

Both size and shape of *Paraethomys* display a strong relationship with the climatic record (correlation of smoothed  $\delta^{18}\text{O}$  curve with *Paraethomys* molar size:  $r^2 = 0.951$ ,  $p < 0.001$ ; with molar shape:  $r^2 = 0.924$ ,  $p < 0.001$ ). Such a relationship suggests that climate may have

played an important role in influencing the evolution of *Paraethomys*. A detailed look at the curve reveals several major phases of environmental change. After the early Pliocene, which is generally considered to be a time of fairly stable climate (Keigwin 1982; Hodell and Kennett 1986), the first cooling event began at approximately 3.1 Ma. Cooling was associated with a change in the global climate regime and the inception of periodic growth and decay of large Northern Hemisphere continental ice sheets (Shackleton and Opdyke 1977; Thunell et al. 1991). A second cooling phase at approximately 2.4 Ma (Backman 1979) corresponds to significant ice growth in the Northern Hemisphere and ice rafting in the North Atlantic. This second cooling trend is particularly marked at the Pliocene/Pleistocene boundary (Thunell et al. 1991). These changes in the global climate regime had a major impact on the climate of the Mediterranean region, where major floral changes indicate increased aridity occurring in southern Europe at about 3.1 Ma and again at about 2.4 Ma (Suc and Zagwijn 1983; Suc 1984).

This increase in aridity probably acted as a selective agent on *Paraethomys*. No trend to-

TABLE 2. Time interval, intervals in size ( $a_0$ ) and shape ( $PC_1$ ), and evolutionary rates of size and shape for successive pairs of deposits.

Interval	$\Delta T$	$\Delta a_0$	$\Delta PC_1$	$\Delta a_0/\Delta T$	$\Delta PC_1/\Delta T$	Res $a_0$
WAN/KEO	0.10	0.08	0.12	0.81	1.17	-0.28
KEO/AMA2	0.10	0.08	0.18	0.78	1.78	-0.31
AMA2/AZB	2.30	0.02	0.85	0.01	0.37	-0.62
AZB/AF8	0.10	0.12	0.08	1.18	0.84	0.02
AF8/AMA3	2.30	0.07	0.46	0.03	0.20	0.28
AMA3/SABH	1.40	0.26	3.18	1.18	2.27	1.19
SABH/IDV	0.50	0.08	1.14	0.16	2.27	0.04
IDV/SABD	0.10	0.07	0.03	0.70	0.30	-0.39
SABD/IRHN	0.30	0.09	1.04	0.31	3.45	0.06

ward the development of stephanodonty is reported in KEO, AMA2 (Jaeger 1977), or AZB (Benammi et al. 1995), and at this time *Paraethomys* was probably still adapted to an environment of closed vegetation. By contrast, stephanodonty is well developed in the Pleistocene *Paraethomys* (Jaeger et al. 1975), suggesting that these rodents ate more grass, which would have characterized the open vegetation resulting from increasing aridity. The changes in the molar outlines can be related to modifications of the tooth associated with the development of this dental specialization (Renaud et al. 1996). Consequently, we interpret the morphological changes between the Mio-Pliocene and Pleistocene rodents observed in this study as an adaptive trend in response to changing diet, climate, and vegetation. Since molar size is related to body size in rodents (Legendre 1989), the observed size increase (Fig. 6A) can be related to decreasing temperature associated with increasing aridity. Such trends toward larger size in mammals during colder times have already been reported in other fossil lineages (Bown et al. 1994) and can be considered as corresponding to Bergmann's rule of increasing mammalian body size with decreasing temperature. However, the increase of the molar size together with the development of the stephanodonty may also be related to increased masticatory efficiency.

#### Timing of the Evolutionary Response of *Paraethomys* to Climatic Changes

The estimate of timing of the evolutionary response of *Paraethomys* to climatic changes is hindered by uncertainties on the age of the fossiliferous deposits, and by the distribution

in time of the localities, restricting discussion to the response to the first cooling event (3.1 Ma). The others (2.4 and 1.7 Ma) occur between the samples of AMA3 and SABH (Fig. 6). Given the age provided for AMA3 (2.9 Ma), this deposit appears to be slightly younger than the first cooling phase. No shape change had occurred yet, but the size, slightly larger than in previous deposits, may correspond to the inception of the evolutionary response to the cooling trend.

To assess the timing of this evolutionary response better, we quantified evolutionary rates along the lineage (Table 2, Fig. 7). Because the use of "haldanes" (Gingerich 1993) requires the estimate of the organism's generation time, we preferred to use "darwins" (Haldane 1949). The evolutionary rate in darwins between two successive samples of means  $x_1$  and  $x_2$  is calculated as

$$(\ln x_2 - \ln x_1)/\text{time interval (m.y.).} \quad (3)$$

Since our shape variable corresponding to coordinates on  $PC_1$  of the upper molar displays negative values hindering the log-transformation, the formula was modified and rates of shape evolution were calculated according to the formula

$$(x_2 - x_1)/\text{time interval (m.y.).} \quad (4)$$

Rates of shape evolution appear to be higher at the Pliocene–Pleistocene transition and during the subsequent period than during the Mio-Pliocene (Fig. 7C). In contrast, no clear pattern emerges from the evolutionary rates of size change, except some very high rates during the Miocene and the Pleistocene, which are due to the very short time interval between two samples. Calculating rates across a

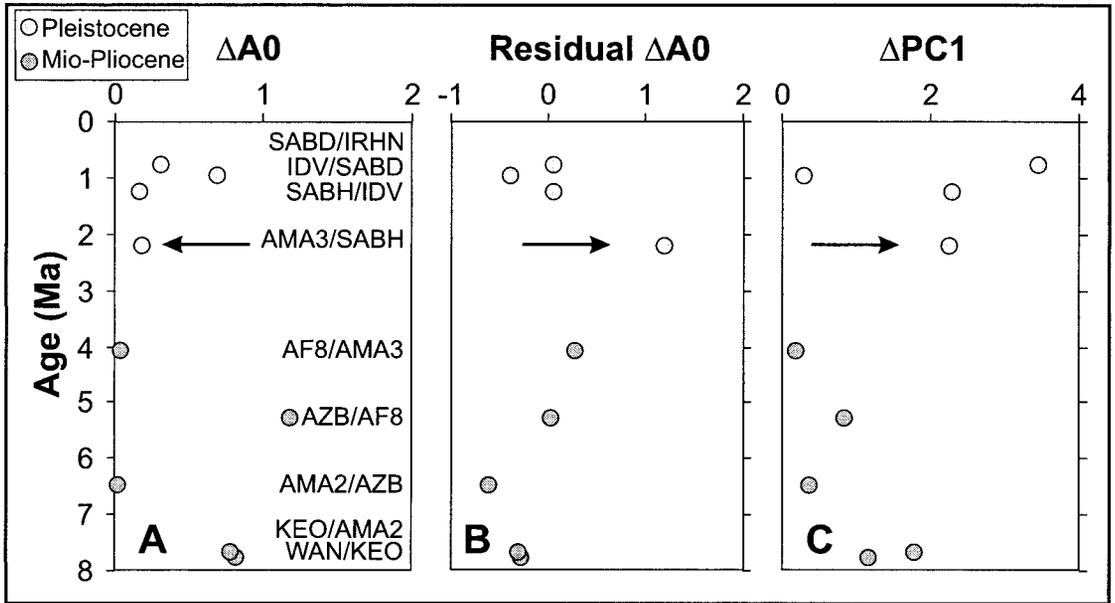


FIGURE 7. Evolutionary rates of size and shape change along the *Paraethomys* lineage. Age corresponds to the mean age of two successive deposits. A, Evolutionary rates in size (estimated by  $a_0$ ), in darwin  $[(\ln x_2 - \ln x_1)/\text{time interval (m.y.)}]$  between successive samples. B, Scaled evolutionary rates in size, estimated by the residuals around the log-log relationship between evolutionary rates in darwin and time interval. C, Evolutionary rates in shape (estimated by PC1)  $[(x_2 - x_1)/\text{time interval (m.y.)}]$ .

longer time interval misses the small frequency fluctuations in rate and direction of evolution, and thus decreases the apparent evolutionary rates. Such a relationship between observed evolutionary rates and time interval can interfere with the comparison of evolutionary rates (Gingerich 1983). This effect is important in our study since the time interval between successive samples varies from 0.1 to several million years. Following Gingerich (1983), we compared the logarithm of the evolutionary rates with the logarithm of the time interval. Size appears to be sensitive to this scaling effect  $(\ln [\Delta A_0/\Delta T \text{ (in darwins)}] = -2.6 - 1.1 \ln \Delta T, r^2 = 0.857, p < 0.001)$ , and despite the few points available for the correlation, the slope of the relationship is comparable to the slope of  $-1.0$  given in Gingerich (1983). To make valid comparisons of evolutionary rates of size change along the lineage, we thus considered the residuals around the log-log correlation between rate and time interval (Fig. 7B). The evolutionary rate corresponding to the transition AMA3–SABH appears to be more than three times higher than the background evolutionary rate, showing

that this particular size increase cannot be explained by the overall trend occurring during the Mio-Pliocene. In that way it supports the hypothesis of an acceleration of size evolution around the Pliocene/Pleistocene boundary.

In contrast, no significant log-log correlation between rate and time interval exists for evolutionary rates of shape ( $r^2 = 0.062, p < 0.518$ ). No significant log-log correlation suggests that the evolution in shape displays a less fractal pattern than evolution in size. Evolution in shape is characterized by more common stasis periods and seems to be insensitive to short-term variations of evolutionary rates. Different evolutionary mechanisms could be responsible for this discrepancy between size and shape. 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 be under the genetic control of a few developmental genes (Whiting and Wheeler 1994). Such a discrepancy between the constraints and determinism acting on size and shape can lead to different evolutionary patterns (Renaud et al. 1996). Size could be more sensitive to small-

scale environmental variations causing small-scale variations in evolutionary rates. Shape evolution would be more buffered with respect to short-term environmental variations. However, both size and shape appear to be sensitive to long-term environmental trends.

#### Comparison with Models of Interaction between Climate and Evolution

The results presented here support the idea of an important influence of climate in triggering morphological evolution in *Paraethomys*. The evolutionary response is possibly adaptive and could be modulated by internal factors such as genetic determination of the different characters. Recently, two main models of interaction between evolution and the environment have been proposed (Vrba 1992, 1995; Sheldon 1993, 1996) and it is useful to compare our results with the predictions of these models.

The "habitat theory" proposed by Vrba (1992, 1995) is based on several hypotheses about the response of clades at different latitudes to Plio-Pleistocene climatic cycles. This model particularly suggests that speciation and extinction are triggered by environmental changes, which should therefore be coincident with periods of turnover in the composition of ecological communities. This model is rather focused on macroevolutionary patterns, and it seems irrelevant to apply this model to our results, which have a different temporal and phylogenetic scale.

The "Plus ça change, plus c'est la même chose" model (Sheldon 1993, 1996) seems to be more relevant to *Paraethomys* evolution, since this model focuses on the evolutionary response of species to varying environments. According to this model, widely fluctuating environments should favor stasis, since successive opposite environmental variations should be unfavorable to adaptations to previous conditions. Furthermore, variable environments may be stressful and the energetic costs of mere survival in such conditions could preclude major evolutionary changes (Parsons 1993). Finally, species may be able to escape stress simply by geographically tracking their usual environment. However, from time to time, a threshold in the environmental

conditions might occur and trigger evolutionary changes. In contrast, stable environments should be characterized by more specialized lineages, which must undergo more constant evolutionary changes. In such environments, therefore, gradual evolution should be favored.

Because of its geographical isolation, trapped between desert and sea, *Paraethomys* could not have escaped environmental stress caused by the onset of Plio-Pleistocene cooling and aridification. Environmental change would thus have triggered an acceleration of morphological evolution. In that respect, the evolution of *Paraethomys* matches the case of variable environments in the "plus ça change" model. However, this model does not explain morphological stasis observed during the stable period of the Mio-Pliocene. The case of *Paraethomys* thus provides arguments both for and against the "plus ça change" model. It does not, however, constitute a definitive test of this model, which may be difficult to test because of the difficulty of determining how variable and stressful past environments were to organisms that are now extinct.

#### Conclusion

The morphometric analysis of the *Paraethomys* lineage has shown that Mio-Pliocene and Pleistocene *Paraethomys* are strongly differentiated by size and shape. This differentiation coincides with and may be an evolutionary response to the onset of Plio-Pleistocene climatic fluctuations. Climate would have strongly influenced rate and direction of *Paraethomys* evolution, since shape changes associated with cooling and aridification may be related to the development of a dental specialization allowing a more grass-eating diet. The observed size increase is in agreement with decreasing temperature, according to Bergmann's rule. The geographic situation of *Paraethomys* prevented it from escaping environmental stress by tracking a more favorable habitat. Consequently, environmental stress resulted in an acceleration of morphological evolution of the species. New deposits and better time control would be necessary for a more precise assessment of the timing of the response of organisms to environmental changes. Isotope anal-

yses on teeth (MacFadden and Shockey 1997) might be a test of the changing diet associated with shape changes in response to cooling and aridification along the Plio-Pleistocene.

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