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Examination of the tooth morphospace of three *Mimomys* lineages (Arvicolinae, Rodentia) by elliptical Fourier methods

Análisis del morfoespacio dental de tres linajes de Mimomys *(Arvicolinae, Rodentia) por medio de métodos elípticos de Fourier*

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Abstract: Morphospaces of three *Mimomys* (Arvicolidae, Rodentia) lineages *(occitanus-ostramosensis/minor-medasensis* and *cappettai-rex*) are examined from the characterization of 180 M_1 occlusal surface outlines using elliptical Fourier methods combined with image analysis techniques. The outlines are characterized by stepwise ordered series of harmonics, each harmonic being described by four parameters termed elliptical descriptors. Divisions within and between species are proposed and tested by discriminant analysis whilst morphological differences between lineages are quantified by Mahalanobis distances. This high-performance method confirms phyletic gradualism observed within the *occitanus-stehlini-polonicus* lineage and seems to be an appropriate morphometric technique for distinguishing between the complex tooth shapes of the various rodent lineages.
Key words: Rodentia, Arvicolinae, Morphology, Fourier shape analysis

Resumen: Los morfoespacios de tres linajes de *Mimomys* (Arvicolidae, Rodentia) *(occitanus-ostramosensis/minor-medasensis* and *cappettai-rex*) son analizados por medio de la caracterización del perímetro de la superficie oclusal de 180 M_1 usando métodos elípticos de Fourier combinados con técnicas de análisis de imágenes. Dicho perímetro es caracterizado por medio de ordenaciones por pasos de series armónicas, siendo cada armónico descrito por cuatro parámetros llamados desciptores elípticos. Se proponen divisiones dentro y entre especies las cuales son contrastadas por medio de análisis discriminante mientras que las diferencias morfológicas entre linajes son cuantificadas por medio de la distancia de Mahalanobis. Este método altamente preciso confirma el gradualismo filético observado dentro del linaje *occitanus-stehlini-polonicus* y parece ser una técnica morfométrica apropiada para distinguir entre las complejas formas dentales de los diferentes linajes de roedores.
Palabras clave : Rodentia, Arvicolinae, Morfología, análisis de Fourier de la forma

INTRODUCTION

Voles (Arvicolinae, Rodentia) are very abundant in the Plio-Pleistocene fossil record (HINTON 1926; CHALINE 1972, 1987; CHALINE *et al*., 1999). Populations can be compared in biometric studies by using increasingly comprehensive morphometries (CHALINE and LAURIN, 1986; BRUNET-LECOMTE, 1988; BRUNET-LECOMTE and CHALINE, 1991). Recent studies have used image analysis of the occlusal surfaces of

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teeth (SCHMIDT-KITTLER, 1984, 1986; VIRIOT *et al*., 1990, 1993). New methods of morphological geometry are now employed (SNEATH, 1967; ROHLF and BOOKSTEIN, 1990; BOOKSTEIN, 1991) using Procrustes (DAVID and LAURIN, 1992) to quantify phenetic anatomical differences and convergence, for example between skulls (COURANT et al., 1997).

The purpose of this paper is to examine the teeth morphospaces of three *Mimomys* lineages (Arvicolidae, Rodentia) by elliptical Fourier methods (KUHL and GIARDINA, 1982) in order to characterize complex morphologies for distinguishing between intra- and interspecific morphological variations.

THE *MIMOMYS OCCITANUS – POLONICUS – OSTRAMOSENSIS* LINEAGE.

Among the 140 lineages identified for the Plio-Pleistocene period, the Eurasian water vole lineage, extending from *Mimomys occitanus* - *M. polonicus* - *M. pliocaenicus* to *M. ostramosensis,* is one of the most interesting for evolution and biostratigraphy (FEJFAR and HEINRICH 1990; FORSYTH MAJOR, 1902; HINTON 1926; KORMOS 1931; HEIM de BALSAC and GUISLAIN 1955; THALER 1955; KOWALSKI 1960; CHALINE and MICHAUX 1969, 1974, 1975; JANOSSY 1974; KRETZOI 1954, 1969; CHALINE 1974, 1984, 1987; JANOSSY and MEULEN 1975; van der WEERD 1978). This lineage is a chronomorphocline that stretches from Western Europe (Spain and England) to Siberia and even China (ZHENG and LI 1986). This vast range means that the lineage is a yardstick in Eurasia for establishing a high-resolution biostratigraphy of the Pliocene and Lower Pleistocene (CHALINE 1989; CHALINE and FARJANEL 1990).

This lineage has also been used for quantitative testing of phyletic gradualism at a European scale. CHALINE and LAURIN (1986), CHALINE et al. (1993) using morphometric methods showed that its evolution involved (1) morphological changes in the occlusal surface of the first lower molar (*Mimomys* ridge, enamel islet), (2) appearance of cement in the re-entrant angles, and, above all (3) a rapid, though irregular, increase in the rate of hypsodonty conveyed by the increased height of the *linea sinuosa* on the crown sides and (4) by the non-appearance of roots. Digital image processing was also applied to area quantification (VIRIOT 1989; VIRIOT *et al.* 1990; VIRIOT *et al.* 1993).

MIMOMYS MINOR – MEDASENSIS AND *MIMOMYS CAPPETTAI – REX* LINEAGES

We added to the study two other lineages. The *Mimomys cappettai - rex* lineage shows the same morphological gradual but diachronic evolution parallel to that of the *M. occitanus hajnackensis* to *M. ostramosensis* lineage, but in the mediterranean region (MICHAUX, 1971). The *Mimomys minor - medasensis* lineage exhibits also the same parallel gradual evolution in western and central Europe, but it is diachronic compared with the previous two other lineages (CHALINE and MICHAUX, 1982).

There is in fact a general trend in primitive rooted arvicolid teeth, a diachronic and irregular increase in the rate of hypsodonty and consequently, the non-appearance of roots leading to the modern unrooted arvicolid teeth (CHALINE, 1987).

For our methodological purpose restricted to the distinction of wearing stages within species and lineages, and to the test of the elliptical Fourier method on some species, we do not use the complete lineages, but only some characteristic species of the three lineages, respectively *Mimomys occitanus-polonicus*, *Mimomys minor* and *Mimomys cappettai*.

MATERIAL

To test the method the following species and populations were subjected to morphometric analyses (teeth drawings by J. CHALINE).

- *Mimomys occitanus* THALER, 1955, from Sète (Hérault, France): 47 specimens (15 juvenile, 22 adult, 10 senile);

- *Mimomys stehlini* KORMOS, 1931 (= *Mimomys occitanus hajnackensis* in Chaline and Farjanel 1990; = *M. hassiacus* HELLER, 1936 in FEJFAR and REPENNING 1998; revised in DAHLMANN, 2001), from Wölfersheim (Germany): 55 specimens (21 juvenile , 29 adult and 5 senile);

- *Mimomys polonicus* KOWALSKI, 1960, from Rebielice Krolewski 1 [4 specimens (1 juvenile, and 3 adult)] and Rebielice Krolewski 2 [18 specimens (3 juvenile, 12 adult, and 3 senile)(Poland)]. This *Mimomys* has been found in Praetiglian cold beds dated between 2.5 and 2.3 Myrs (ZAGWIJN, 1974).

- *Mimomys minor* FEJFAR, 1961 *(= M. septimanus* Michaux, 1971), 11 specimens from Balaruc 2 (3 juvenile, 7 adult, and 1 senile); 21 specimens from

Seynes (7 juvenile, 10 adult, and 4 senile)(France);

-*Mimomys cappettai* MICHAUX, 1971, and Balaruc 2 (France): 18 specimens (3 juvenile, 7 adult, 8 senile);

- *Dolomys adroveri* FEJFAR, MEIN and MOISSENET, 1990 from Orrios 3 (Spain): 10 specimens (4 juvenile, 4 adult, 2 senile).

The population localities are dated from Middle to Upper Pliocene: Orrios 3 (4 Myrs), Sète (3.5 Myrs), Wölfersheim (3.4 Myrs), Balaruc 2 (3.2 Myrs), Seynes (2.8 Myrs), and Rebielice 1 and 2 (2.5 Myrs).

METHOD

PROCEDURE OF PROCESSING AND IMAGE ANALYSIS

The outlines were extracted from the original drawings. Only the enamel external outline of the occlusal surface was given full consideration for the analysis continuation. A procedure was developed for converting the outline data into an ordered list of Cartesian coordinates (x, y) representative of the points describing the outline. For each outline, three types of standardization were performed successively. Standardization of size so as to take into account only the outline shape. For that, the interior area delimited by each outline was scaled to unity. Angular standardization, whereby outlines were reoriented and aligned so that the disto-mesial diameter corresponded to the ordinate axis of the reference landmark. Lastly, a standardization of the first point position of the outline, the first point of each outline being moved on the posterior loop in order to correspond to the ordinate axis of the reference landmark.

ELLIPTICAL FOURIER ANALYSIS

The coordinates of each point of the outline were expressed according to their position on the outline. The abscissa (x) and the ordinates (y) of each point were thus expressed in terms of the curvilinear coordinate (t) of this same point; this new expression allowing an outline description by two discrete parametric functions x(t) and y(t). These x(t) and y(t) functions were calculated for a series of 512 points distributed around the entire occclusal outline.

The elliptic Fourier analysis program was developed in Visual C++ language by SCHMITTBUHL *et al.* (1995, 1997). The outline represented by the parametric functions x(t) and y(t) could be broken up into a Fourier series (KUHL & GIARDINA, 1982). The mathematical expression of this series is:

$$x(t) = A_0 + \sum_{n=1}^{k} a_n \cos(nt) + \sum_{n=1}^{k} b_n \sin(nt)$$

$$y(t) = C_0 + \sum_{n=1}^{k} c_n \cos(nt) + \sum_{n=1}^{k} d_n \sin(nt)$$

Where A0 and C0 are the constant terms, an, bn, cn, dn correspond to the adjusted Fourier coefficients and k represents the number of harmonics used. The pairs of coefficents (an, bn) and (cn, dn) each define a harmonic of frequency n. The geometric representation of each harmonic pair of order n could be represented as an ellipse (KUHL & GIARDINA, 1982; SCHMITTBUHL *et al.*, 1997, 2001). From this geometric representation, each ellipse was described by four new parameters termed elliptic descriptors (SCHMITTBUHL *et al.*, 1997, 2001, 2001a, b). These parameters correspond to the half-length of the major axis of the nth ellipse, the half-length of the minor axis of the nth ellipse, the angle of rotation corresponding to the length axis orientation of the nth ellipse, and the angle of phase corresponding to the position of the first point on the nth ellipse, respectively.

RECONSTRUCTION OF THE OCCLUSAL OUTLINE

The occlusal outlines were reconstructed step by step using an increasing number of harmonics (Fig. 1).

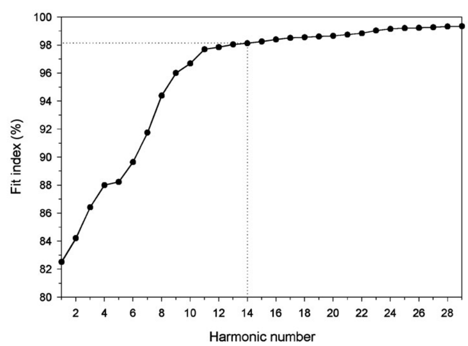

Figure 1.- Convergence index of standardized occlusal surfaces of *M. cappettai* (Balaruc 2, France) for the 29 first harmonics.
Figura 1.- Índice de convergencia de superficies oclusales estandarizadas de M. cappettai *(Balaruc 2, France) para los primeros 29 armónicos.*

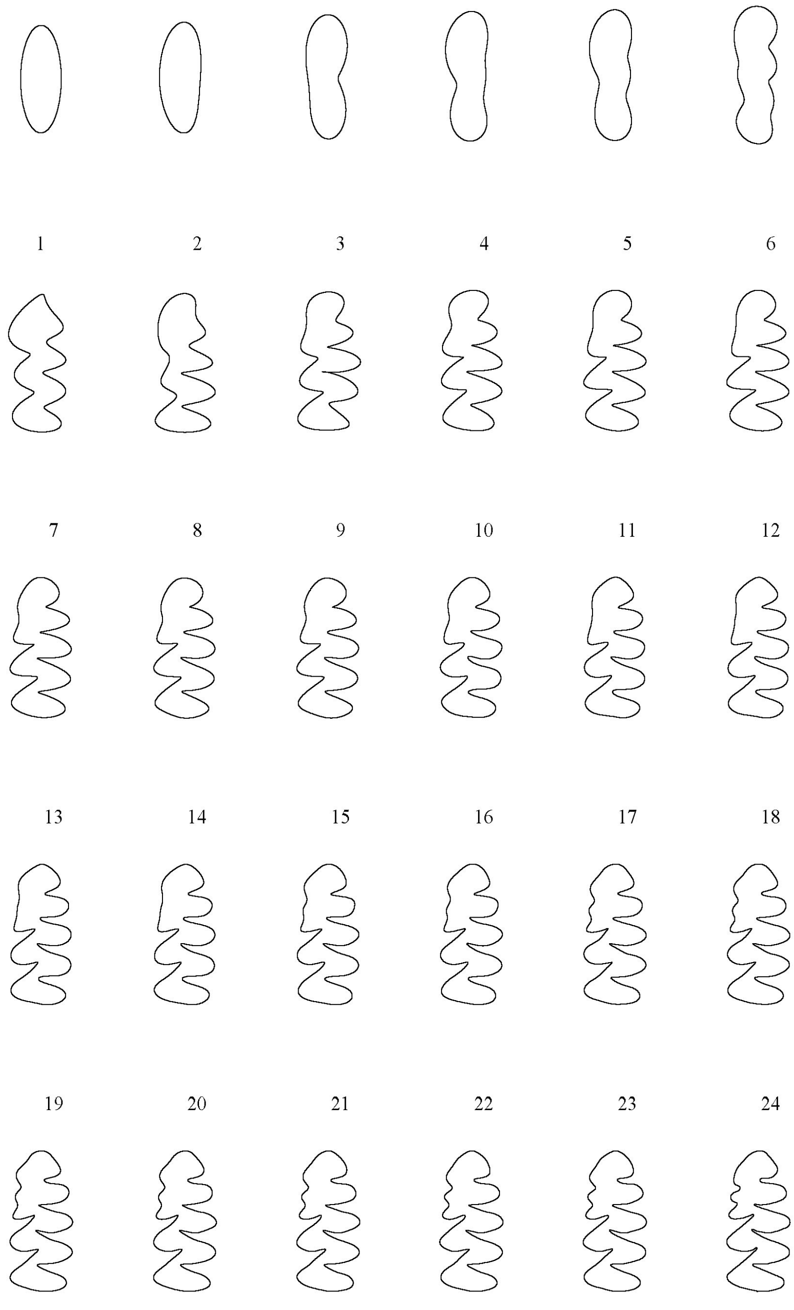

Figure 2.- Example of outline reconstruction for a specimen of M_1 of *M. cappettai* (Balaruc 2, France) using an increasing number of harmonics (1 to 29).
Figura 2.- Ejemplo de reconstrucción del perímetro de un espécimen de M_1 de M. cappettai (Balaruc 2, Francia) usando un número de armónicos en incremento (1 a 29).

These reconstructions were carried out point by point, and corresponded to the summing of vectors; each vector having its origin at the center of the ellipse and its end on the outline of the ellipse considered.

STATISTICAL ANALYSIS OF THE FOURIER ELLIPTIC DESCRIPTORS

Discriminant analyses were carried out by using an increasing number of elliptic descriptors (the first 14 harmonics, which allowed 98% of the original outline to be reconstructed; Fig. 2). Only descriptors characterizing the ellipse geometrically (values of large and small semi-axis and orientation of the ellipse) have been retained for the analysis. The statistical level of significance for each discriminating analysis was evaluated by the Wilk's Lambda test (KLECKA, 1980). The result of each discriminating analysis was represented on a two-dimensional graph, defined by the first two discriminating axes. For each samples, the series of individuals were represented by a scatter plot. The centroid of each cloud was determined, and the Mahalanobis distances (KLECKA, 1980; SHARMA, 1996) between centroids were given.

RESULTS AND DISCUSSION

Our methodological aim is to test whether the elliptic descriptors of Fourier are able: (1) to separate the M_1 main teeth wearing stages (i.e. juvenile, adult, and senile) of all species from all localities; (2) to distinguish between the complex shapes of the studied lineages; and (3) to morphometrically characte-

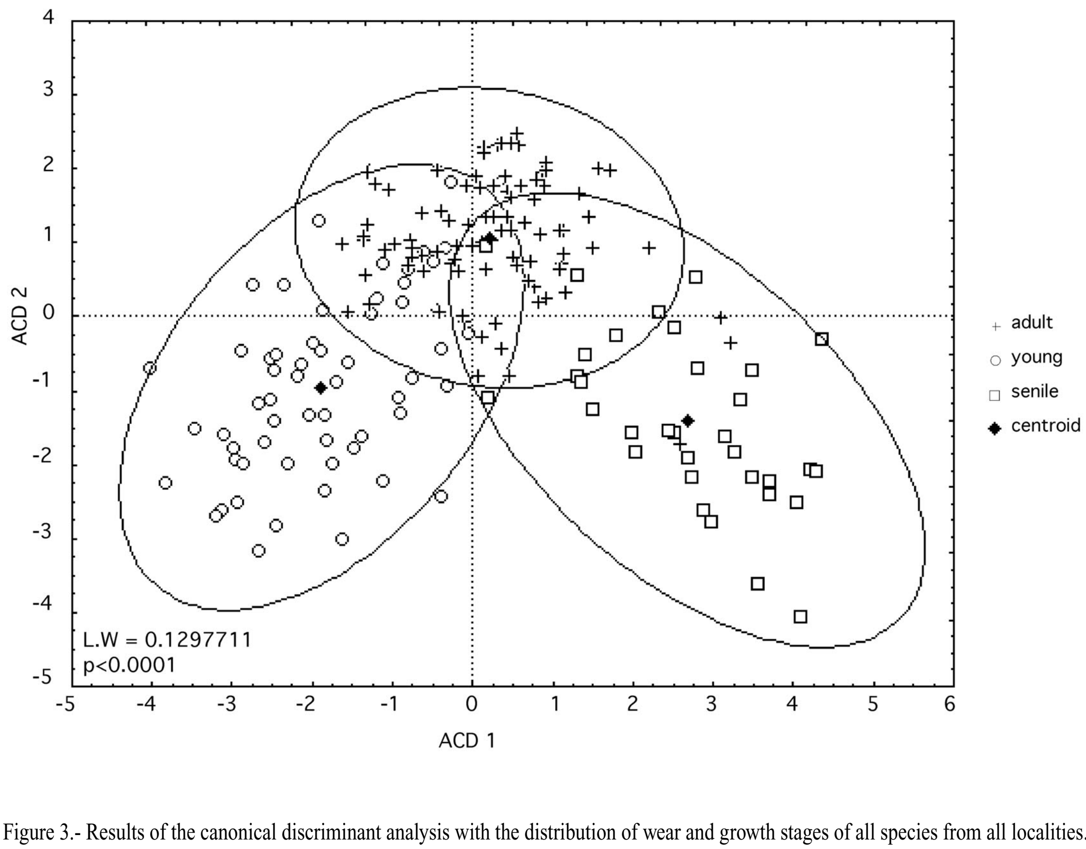

Figure 3.- Results of the canonical discriminant analysis with the distribution of wear and growth stages of all species from all localities. Wilk's Lambda (L.W), associated probability (p), and p<0.05 ellipses of confidence for each group are provided.

Figura 3.- Resultados del análisis canónico discriminante con la distribución de los estadíos de desgaste y crecimiento de todas las especies de todas las localidades. Se proporcionan el valor de Lambda de Wilk (L.W), la probabilidad asociada (p), y las elipses de confianza (p<0.05) para cada grupo.

rize the gradual evolution of these lineages demonstrated by other methods.

	Senile	Adult	Young	% of correct classification
Young	21,336	8,610	0	78,95
Adult	12,378	0	*****	94,68
Senile	0	*****	*****	87,88

Table 1.- Mahalanobis distances between centroids of wear and growth stages (all species). p levels are given with the following significance: --: p>0.5; -: p>0.05; *: p<0.05; **: p<0.01; ***: p<0.001 ; ****: p<0.0001 ; *****: p<0.00001. The percentages of correct reassigments are also provided.
Tabla 1.- Distancias de Mahalanobis entre los centroides de los estadíos de desgaste y crecimiento (todas las especies). También se proporcionan los porcentajes de asignación correcta.

In a first approach (Fig. 3), independently of the species and localities concerned, the morphological pattern of growth and wear stages (juvenile, adult, and senile) is clearly demonstrated. The Mahalanobis distances between the centroids of each stage are significantly distinct (Table 1). Thus, it is always possible to separate the three major wear stages of M_1. For the following analysis we retain only the adult specimens.

Figure 4 shows the morphological field of each species from their different localities. It is clear that all species can be distinguished by this method. *Dolomys adroveri* is clearly separated from the other derived species of *Mimomys minor* and *M. cappettai*. These two species, which occur in Balaruc 2, are well distinguished. The two *M. minor* populations from Balaruc 2 and Seynes can also be separated, despite being closely related in the time sequence and closely related morphologically. All Mahalonobis distances are significant between each centroid of the different populations (table 2).

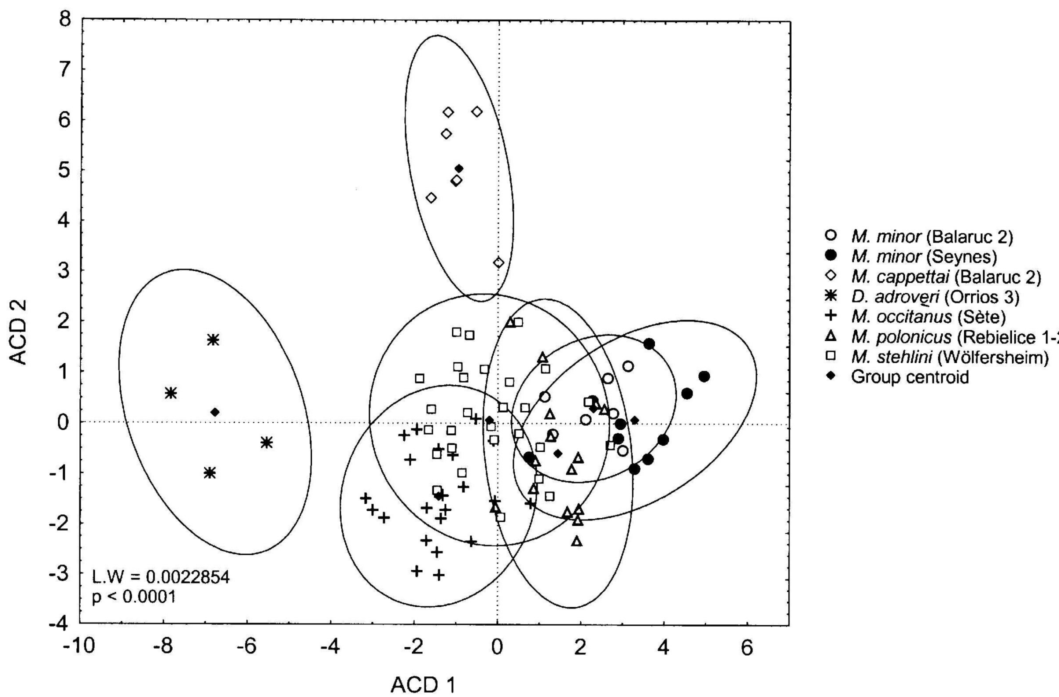

Figure 4.- Results of the canonical discriminant analysis showing the distribution of the species (only adult teeth) from each locality on the plot defined by discriminant functions 1 and 2. Wilk's Lambda (L.W), associated probability (p), and p<0.05 ellipses of confidence for each group are provided.
Figura 4.- Resultados del análisis canónico discriminante mostrando la distribución de las especies (sólo dientes adultos) de cada localidad sobre el gráfico definido por las funciones discriminantes 1 y 2. Se proporcionan el valor de Lambda de Wilk (L.W), la probabilidad asociada (p), y las elipses de confianza (p<0.05) para cada grupo.

	***M. stehlini* (Wölfersheim)**	***M. polonicus* (Rebielice 1-2)**	***M. occitanus* (Sète)**	***D. adroveri* (Orrios 3)**	***M. cappettai* (Balaruc 2)**	***M. minor* (Seynes)**	***M. minor* (Balaruc 2)**	**% of correct classificatio**
***M. minor* (Balaruc 2)**	20,115	15,755	27,727	104,263	46,530	14,053	0	71,43
***M. minor* (Seynes)**	24,049	25,034	36,721	121,191	59,065	0	- -	80,00
***M. cappettai* (Balaruc 2)**	36,843	47,317	46,551	91,227	0	***	-	100
***D. adroveri* (Orrios 3)**	70,853	95,846	62,840	0	**	****	***	100
***M. occitanus* (Sète)**	12,601	19,845	0	**	***	***	-	90,91
***M. polonicus* (Rebielice 1-2)**	16,638	0	**	***	**	*	- -	100
***M. stehlini* (Wölfersheim)**	0	*	*	**	**	**	- -	96,55

Table 2.- Mahalanobis distances between centroids of each species (only adult teeth, not severely worn) from each locality. p levels and percentages of correct reassigments are provided. For p levels significance, see table 1.
Tabla 2.- Distancias de Mahalanobis entre los centroides de cada especie (sólo dientes adultos no severamente desgastados) de cada localidad. Se proporcionan los niveles de significación (p) y los porcentajes de asignación correcta. Para los niveles de significación de p veáse Tabla 1.

	***M. stehlini* (Wölfersheim)**	***M. polonicus* (Rebielice 1-2)**	***M. occitanus* (Sète)**	**% of correct classification**
***M. occitanus* (Sète)**	22,145	40,823	0	100
***M. polonicus* (Rebielice 1-2)**	19,625	0	**	100
***M. stehlini* (Wölfersheim)**	0	-	*	100

Table 3.- Mahalanobis distances between centroids of the three species (only adult teeth, not severely worn) from the *Mimomys occitanus - stehlini – polonicus* lineage. p levels and percentages of correct reassigments are provided. For p levels significance, see table 1.
Tabla 3.- Distancias de Mahalanobis entre los centroides de la tres especies (sólo dientes adultos no severamente desgastados) del linaje Mimomys occitanus - stehlini – polonicus*. Se proporcionan los niveles de significación (p) y los porcentajes de asignación correcta. Para los niveles de significación de p veáse Tabla 1.*

Finally, the three populations of the *M. occitanus-stehlini-polonicus* lineage constitute a homogeneous set separated from the other two lineages of *M. minor* and *M. cappettai*. But within this set, all three original populations can be distinguished as shown in figure 5 and table 3. Morever, the gradual evolution of this lineage, previously demonstrated by multivariate analysis (CHALINE and LAURIN, 1986) and by image analysis (VIRIOT *et al.,* 1990, 1993; NERAUDEAU *et al.,* 1995) is confirmed by this new study based on the Fourier elliptic descriptors of tooth shape.

CONCLUSION

The Fourier elliptic method has good power for discriminating among wear stages, fossil populations, evolutionary lineage stages, and locality characteristics.

This method is certainly one of the most appropriate because it concerns only the morphological signal described by the teeth outlines independently of any size effects.

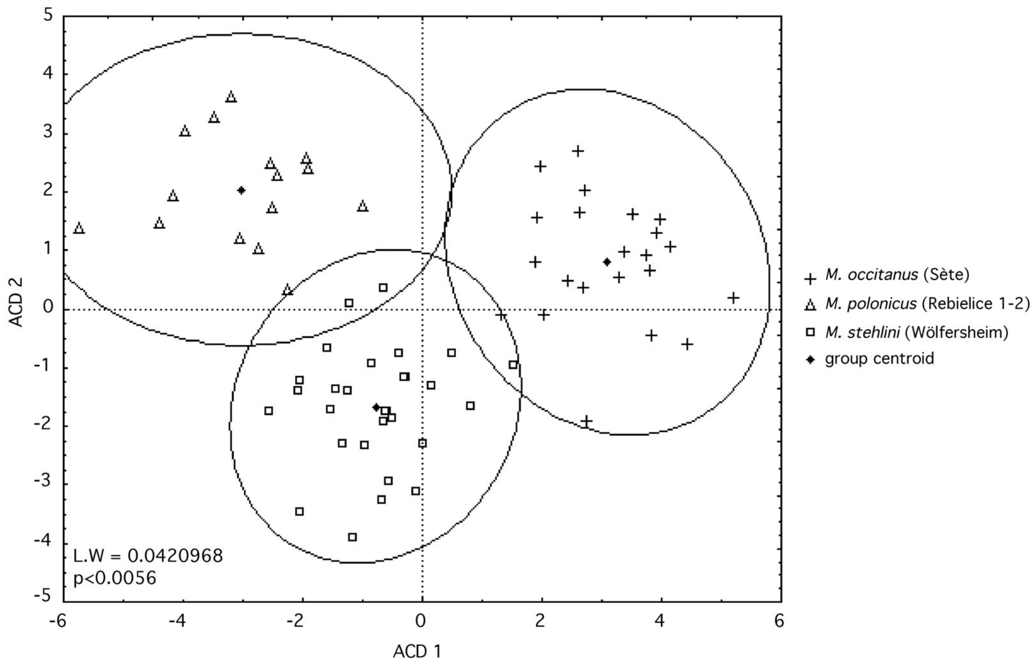

Figure 5: Results of the canonical discriminant analysis with the distribution of the three species (only adult teeth) of the *Mimomys occitanus - stehlini – polonicus* lineage. Wilk's Lambda (L.W), associated probability (p), and p<0.05 ellipses of confidence for each group are provided.

Figura 5.- Resultados del análisis canónico discriminante con la distribución de las tres especies (sólo dientes adultos) del linaje Mimomys occitanus - stehlini – polonicus . *Se proporcionan el valor de Lambda de Wilk (L.W), la probabilidad asociada (p), y las elipses de confianza (p<0.05) para cada grupo.*

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REFERENCES

Bookstein, F.L. 1991. Morphometric tools for landmark data. Geometry and biology. 435pp. Cambridge University Press. New-York.

Brunet-Lecomte, P. 1988. "Les campagnols souterrains (*Terricola*, Arvicolinae, Rodentia) actuels et fossiles d'Europe occidentale". 146pp. Thèse Université de Bourgogne, Dijon (unpublished).

Brunet-Lecomte, P. & Chaline, J. 1991. Morphological evolution and phylogenetic relationships of the European ground voles (Arvicolinae, Rodentia). *Lethaia*, **24**: 45-53.

Chaline, J. 1972. Les rongeurs du Pléistocène moyen et supérieur de France. 410 pp. Cahiers de Paléontologie. CNRS, Paris,

Chaline, J. 1974. Un nouveau critère d'étude des *Mimomys*, et les rapports de *Mimomys occitanus, Mimomys stehlini* et de *Mimomys polonicus* (Arvicolidae, Rodentia). *Acta Zoologica Cracoviensia*, **19(16)**: 337-356.

Chaline, J. 1984. La séquence des rongeurs de Bresse en tant que référence biostratigraphique et climatique. *Géologie de la France*, BRGM, **3**: 251-268,

Chaline, J. 1987. Arvicolid Data (Arvicolidae, Rodentia) and Evolutionary Concepts. *Evolutionary Biology*, **21**: 237-310.

Chaline, J. & Farjanel, G. 1990. Plio-Pleistocene rodent biostratigraphy and palynology of the Bresse Basin, France and correlations within western Europe. *Boreas*, **19**: 69-80.

Chaline, J. & Michaux, J. 1969. Evolution et signification stratigraphique des Arvicolidés du genre *Mimomys* dans le Plio-Pléistocène de France. *Comptes Rendus Académie des Sciences*, Paris, **268(D)**: 3029-3032.

CHALINE, J. & MICHAUX, J. 1974. Les micromammifères et la biostratigraphie de la bordure occidentale du remplissage bressan. *Bulletin Scientifique de Bourgogne*, **24**: 55-83.

CHALINE, J. & MICHAUX, J. 1975. Les rongeurs du Pléistocène de France. *Mémoire du BRGM.*, **78(1)**: 89-97.

CHALINE, J. & MICHAUX, J. 1982. Remarques à propos de mimomys septimanus MICHAUX, 1971 (Rodentia, Mammalia). *Geobios* **15(1)**: 95-96.

CHALINE, J. & LAURIN, B. 1986. Phyletic gradualism in a European Plio-Pleistocene *Mimomys* lineage (Arvicolidae, Rodentia). *Paleobiology*, **12**: 203-216.

CHALINE, J., LAURIN, B., BRUNET-LECOMTE, P. & VIRIOT, L. 1993. Morphological Trends and Rates of Evolution in Arvicolids (Arvicolidae, Rodentia) at species level: toward a Punctuated Equilibria/Disequilibria Model. In*: Modes an tempo of Evolution in the Quaternary*. J. CHALINE & L. WERDELIN, Eds. Pags. 27-39. Quaternary International, 19.

CHALINE, J., BRUNET-LECOMTE, P., MONTUIRE, S., VIRIOT, L. & COURANT, F. 1999. Anatomy of the arvicoline radiation (Rodentia): palaeogeographical, palaeoecological history and evolutionary data. *Ann. Zool. Fennicci*, **36**: 239-267.

COURANT, F., DAVID, B., LAURIN, B. & CHALINE, J. 1997. Quantification of cranial convergences in Arvicolids (Rodentia). *Biological Journal of the Linnean Society*, **62**: 505-517.

DAHLMANN, T. 2001. Die Kleinsäuger der unter-pliozänen Fundstelle Wölfersheim in der Wetterau (Mammalia: Lipotyphla, Chiroptera, Rodentia). *Courier Forschungsinstitut Senkenberg*, **227**:1-129.

DAVID, B. & LAURIN, B. 1992. Procrustes: an interactive program for shape analyses using landmarks. Version 2.0. Université de Bourgogne, Dijon, France.

FEJFAR, O. 1961. Die plio-pleistozänen Wirbeltierfaunen von Hajnacka und Ivanoce (Slowakei). CSR. II. Microtidae und Cricetidae. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie*, *Abhandlungen*, **112**: 48-82.

FEJFAR, O. & HEINRICH, W.-D. (Eds.) 1990. *Evolution, Phylogeny and Biostratigraphy of Arvicolines.* International Symposium, Geological Survey, Praha.

FEJFAR, O., MEIN, P. & MOISSENET, E. 1990. Early arvicolids from the Ruscinian (Early Pliocene) of the Teruel Basin, Spain. In*: International Symposium on Evolution, Phylogeny and Biostratigraphy of Arvicolines.* O. FEJFAR and W.-D. HEINRICH Eds: 133-164. Geological Survey, Praha.

FEJFAR, O. & REPENNING, C.A. 1998. The ancestors of the lemmings (Lemmini, Arvicolinae, Cricetidae, Rodentia) in the early Pliocene of Wölfersheim near Frankfurt am Main; Germany. *Senkenberg. lethaea*,**77(1-2)**:161-193.

FORSYTH MAJOR, C.I. 1902. Some jaws and teeth of Pliocene voles (*Mimomys* gen. nov.), from the Norwich Crag at Thorpe, and from the upper Val d'Arno. *Proceedings of the Zoological Society*, London, **1**: 102-107.

HEIM De BALSAC, H. & GUISLAIN, R. 1955. Évolution et spéciation des Campagnols du genre *Arvicola* en territoire français. *Mammalia*, **19**: 367-390.

HELLER, F. 1936. Eine oberpliocäne Wirbeltierfauna aus Rheinhessen. Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, **76(B)**: 99-158.

HINTON, M.A.C. 1926. Monograph of the Voles and Lemmings (Microtidae) living and extinct. *British Museum Natural History*, **1**: 350-383.

JANOSSY, D. 1974. New "Middle Pliocene" Microvertebrate fauna from Northern Hungary (Osztramos Loc. 9). *Fragmenta Mineralogia et Paleontologia*, **5**: 17-27.

JANOSSY, D. & MEULEN, A.J. van der 1975. On *Mimomys* (Rodentia) from Osztramos 3, north Hungary. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen*, **78(B)**: 381-391.

KLECKA, W.R., 1980. Discriminant analysis. Quantitative applications in the Social Sciences. Sage University papers, Beverly Hills : 71pp.

KORMOS, T. 1931. Oberpliozäne Wühlmäuse von Senèze (Haute-Loire) und Val d'Arno (Toscana). *Abhandlungen der Schweizerrische Paläontologische Geselschaft*, **51**: 1-14.

KOWALSKI, K. 1960. Pliocene insectivores and rodents from Rebielice Krolewski (Poland). *Acta Zoologica Cracoviensia*, **5**: 155-201.

KRETZOI, M. 1954. Bericht über die calabrische villafranchische Fauna von Kislang, Kom. Fejer. Jahrbuch Ungarisches Museum Geologisches Anstalt, 213-265.

KRETZOI, M. 1969. Skizze einer Arvicoliden-Phylogenie-Stand 1969. *Vertebrata Hungarica*, **11(1-2)**: 155-193.

KUHL, F. & GIARDINA, C.R. 1982. Elliptic Fourier features of a closed contour. Comput. *Graph. Image Process*, **18**: 236-258.

MICHAUX, J. 1971. Arvicolinae (Rodentia) du Pliocène terminal et du Quaternaire ancien de France et d'Espagne. *Palaeovertebrata*, Montpellier, **4(5)**: 137-214.

NERAUDEAU, D., VIRIOT, L., CHALINE , J. LAURIN, B. & KOLFSCHOTEN, T. 1995. Discontinuity in the Plio-Pleistocene Eurasian water-vole lineage. *Paleontology*, **38**: 77-85.

ROHLF, F.J., & BOOKSTEIN, F.L. 1990. Proceedings of the Michigan morphometrics workshop. 380pp. University of Michigan Press. Ann Arbor.

SCHMIDT-KITTLER, N. 1984. Pattern analysis of occlusal surfaces in hypsodont herbivores and its bearing on morpho-functional studies. *Proceedings of the Koninklijke Nederlandse Akadademie*, **87(4)**: 453-480.

SCHMIDT-KITTLER, N. 1986. Evaluation of occlusal patterns of hypsodont rodent dentitions by shape parameters. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, Stuttgart, **173(1)**: 75-98.

SCHMITTBUHL, M., ALLENBACH, B., SCHAAF, A. & Le MINOR, J.-M. 1995. Description et classification de formes biologiques par les méthodes de Fourier. In*: Informatique et imagerie médicale*, A. WACKENHEIM & G. ZÖLLNER, Eds. Pags. 85-99. Masson, Paris.

SCHMITTBUHL, M., ALLENBACH, B., SCHAAF, A. & Le MINOR, J.-M. 1997. Méthodes de Fourier elliptique appliquée à la quantification de la forme de contours complexes. *Biométrie Humaine et Anthropologie*, **15**: 233-241.

SCHMITTBUHL, M., ALLENBACH, B., Le MINOR, J.-M. & SCHAAF, A. 2001. Elliptical descriptors : some simplified morphometrics parameters for the quantification of complex outlines. *Mathematical Geology*, in press.

SCHMITTBUHL M., Le MINOR J.M., TARONI F., MANGIN P. 2001a. Sexual dimorphism of the human mandible: demonstration by elliptical Fourier analysis. International *Journal of Legal Medicine*, in press.

SCHMITTBUHL M., Le MINOR J.M., TARONI F., MANGIN P. 2001b. The human mandible in lateral view: elliptical Fourier descriptors of the outline and their morphological analysis. *Annals of Anatomy*, in press.

SHARMA, S. 1996. Applied multivariate techniques. John Wiley & Sons. New York.

SNEATH, PHA. 1967. Trend-surface analysis of transformation grids. *Journal of Zoology*, **151**: 65-122.

THALER, L. 1955. Sur l'âge pliocène de la faune des grottes du Lazaret (Sète, Hérault). *Comptes Rendus Académie des Sciences*, Paris, **240(D)**: 387-398.

VIRIOT, L. 1989. La lignée évolutive *Mimomys davakosi-M. ostramosensis*. Quantification des modifications morphologiques de la surface occlusale à l'aide de l'analyse d'images. 31pp. Mem. DEA, Université de Bourgogne (unpublished).

VIRIOT, L., CHALINE, J. & SCHAAF, A. 1990. Quantification du gradualisme phylétique de *Mimomys occitanus* à *Mimomys ostramosensis* (Arvicolidae, Rodentia) à l'aide de l'analyse d'images. *Comptes Rendus Académie des Sciences*, Paris, **310(D)**:1755-1760.

VIRIOT, L., CHALINE, J., SCHAAF, A. & Le BOULENGÉ, E. 1993. Ontogenetic change of *Ondatra zibethicus* (Arvicolidae, Rodentia) cheek teeth analyzed by digital image processing. In*: Morphological change in Quaternary mammals of North America,* R.A. MARTIN & A.D. BARNOSKY, Eds. pags. 373-391. Univ. Press. Cambridge.

WEERD, A. van der 1978. Early Ruscinian rodents and lagomorphs (Mammalia) from the lignites near Ptolemais (Macedonia, Greece). *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen*, **82(B)**: 127-170.

ZAGWIJN, W. 1974. The Plio-Pleistocene boundary in western and southern Europe. *Boreas*, **3**: 75-97.

ZHENG, S. & LI, C. 1986. A Review of Chinese *Mimomys* (Arvicolidae, Rodentia). *Vertebrata Palasiatica*, **24(2)**: 81-109.