

# Adaptive latitudinal trends in the mandible shape of *Apodemus* wood mice

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## Abstract

**Aim** Size and shape of the mandible are investigated across the latitudinal range of the European wood mouse (*Apodemus sylvaticus*), in order to address the relative importance of genetic structure, insularity, and geographical gradient in patterning morphological variation. Results are compared with those on two Asiatic species of wood mice, *A. argenteus* and *A. speciosus*.

**Location** The European wood mouse is sampled by a set of trapping localities including both, islands and mainland populations, as well as the four genetic groups identified in previous studies. The localities cover a latitudinal gradient from 55° N to 36° N.

**Methods** Different Fourier methods are applied to the outlines of mandibles and their results compared in the case of *A. sylvaticus*. All provide similar results and allow a quantification of the size and shape variations across the geographical range of the European wood mouse. Using the method allowing for the best reduction of the informative data set, a comparison of the European wood mouse with the two Asiatic species was performed.

**Results** Within the European wood mouse *A. sylvaticus*, a strong latitudinal gradient in mandible shape overrides the influence of insularity and genetic structure. Yet, random morphological divergence in insular conditions can be identified as a secondary process of shape differentiation. Size displays no obvious pattern of variation, neither with insularity or latitude. A comparison with two other species of wood mice suggests that a similar latitudinal gradient in mandible shape exists in different species, mandibles being flatter in the north and wider in the south.

**Main conclusion** The latitudinal gradient in mandible shape observed in the three species of wood mice is interpreted as an intraspecific adaptive response to gradual changes in feeding behaviour.

## Keywords

Shape, size, mandible, *Apodemus*, Rodentia, latitude, island biogeography, morphometrics, Fourier analysis.

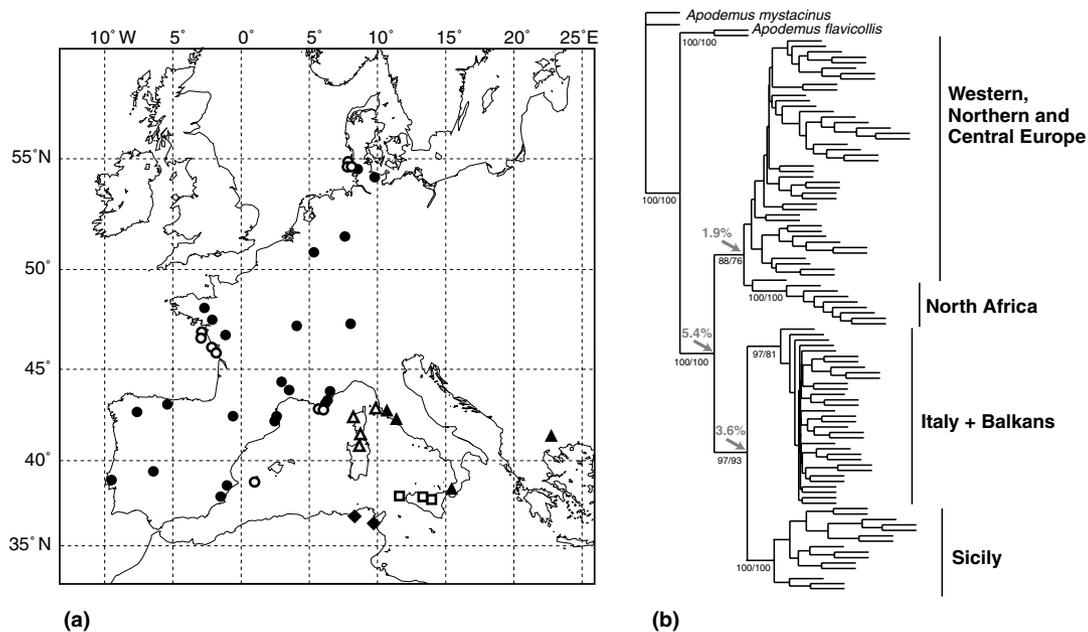
## INTRODUCTION

Size of organisms has long been recognized to display important biogeographical variations. The trend towards an increase in size with latitude, or Bergmann's rule (Bergmann, 1847; Mayr, 1942), has been demonstrated in mammals and

invertebrates (Ray, 1960; Chapelle & Peck, 1999). Size changes can also be the consequence of isolation such as in the islands, where small mammals like rodents will tend to become larger, whereas large mammals tend to be smaller (Foster, 1964; Lomolino, 1985; Michaux *et al.*, 2002b).

Apart from size, the shape of organs is of prime importance in the interaction of the organism with its environment. Taxonomic differentiation is commonly associated with morphological divergence, but patterns of intraspecific variation are less investigated. Still, genetic structure (Auffray *et al.*, 1996; Corti & Rohlf, 2001) and insularity

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**Figure 1** (a) Map showing the sampling localities of the European wood mice (*Apodemus sylvaticus*) considered in this study. Sampling includes mainland (close symbols) and island (open symbols) populations, as well as four different genetic groups (western Europe: circles; Italy/Balkan: triangles; Sicily: square; North Africa: diamond). (b) Neighbour-joining tree, based on mtDNA markers, representing the different genetic groups observed within the European wood mouse. Numbers indicated below the branches correspond to bootstrap supports obtained in neighbour-joining and maximum parsimony analyses, respectively. Numbers indicated above the branches indicate the percentages of genetic divergence (Kimura two parameters estimator) observed between the different genetic groups (after Michaux *et al.*, 2003).

(Berry, 1973) have been observed to cause divergence of cranial morphology in rodents. Geographical gradients have been reported in cranial (Fadda & Corti, 2001), mandibular (Duarte *et al.*, 2000) and dental shape (Renaud, 1999). These factors can interact to various degrees as demonstrated by the latitudinal gradient in mandible morphology observed in two species of wood mice in the Japanese archipelago, where the effects of the environmental gradient interfered with those of insularity (Renaud & Millien, 2001).

In the present study, we investigated the biogeographical morphological variations in the mandible of the European wood mouse, *Apodemus sylvaticus*. Recent genetic analyses based on mitochondrial cytochrome-b sequences and RFLP variations (Michaux *et al.*, 1996b; Libois *et al.*, 2001; Michaux *et al.*, 2003) have allowed two main groups to be identified (Fig. 1). One group includes all animals from western, central and northern Europe whereas the second group comprises animals from Italy and the Balkans. The two groups demonstrated a divergence of *c.* 5% for the cytochrome-b gene, a value similar to that detected between the two sub-species of domestic mice (Ferris *et al.*, 1983a, b; Boursot *et al.*, 1993). This genetic differentiation is interpreted as being the result of repeated isolation during the Quaternary glacial cycles in the two refuge zones formed by the Iberian and Italy/Balkans peninsulas. Following the last glacial maximum, western, northern, and central European regions were recolonized from the Iberian

wood mouse stock population, whereas Italian and Balkan animals remained confined to their zone of origin, as a consequence of the Alpine barrier as well as their low population densities (Michaux *et al.*, 1996b, 1998a, 2003). Within the main clusters, two additional sub-groups have been identified. The first one corresponds to north African wood mice, which are closely related to the Iberian stock, suggesting a recent colonization via the Gibraltar strait (Libois *et al.*, 2001). Secondly, a Sicilian group is related to Italian populations, although an important genetic divergence of 3.2% dates the differentiation event to at least 800,000 years ago (Michaux *et al.*, 1998b; Libois *et al.*, 2001).

Another possible source of morphological variation within *A. sylvaticus* is the existence of various island populations, belonging to different genetic groups. Although colonization of these islands has generally not led to significant genetic divergence from mainland populations (Michaux *et al.*, 1996a, 1998a; Libois *et al.*, 2001), island wood mice, however, often display a larger body size than their closest mainland relatives, suggesting the occurrence of an 'insular syndrome' (Angerbjörn, 1986; Michaux *et al.*, 1996b, 2002b).

The pattern of morphological differentiation in the European wood mouse was, therefore, analysed in the context of genetic, insular, and latitudinal factors, all of which can result in morphological divergence. Mandible shape was estimated by Fourier analyses of the outline and compared

between wood mice from the whole of western Europe (Fig. 1), including specimens from the different genetic groups and various islands.

To test the generality of the results, the morphological pattern observed in the European wood mouse *A. sylvaticus* was compared with that in two other species of wood mice, *A. argenteus* and *A. speciosus*. These sympatric species live in the Japanese archipelago. They differentiated 5.5 Ma, their common ancestor having separated from its European counterpart 8 Ma (Michaux *et al.*, 2002a). Given this ancient divergence from a *A. sylvaticus* ancestor, any pattern of morphological variation in the Japanese wood mice is likely to have developed independently.

## MATERIALS AND METHODS

### Geographical sampling

For *A. sylvaticus*, 442 specimens from localities all over western Europe (Fig. 1) were used, from the collections of the Institut für Haustierkunde (Kiel, Germany), Museum National d'Histoire Naturelle (Paris, France), and the collection of J.R. Michaux. All animals from this latter collection were diagnosed genetically as *A. sylvaticus*. In some localities, a reduced sample size hindered any robust statistical analysis, so these specimens were pooled with those of neighbouring localities (Table 1). Hence, our analysis included twenty-eight localities, or groups of neighbouring localities (average number of specimens per group = 16; maximum = 76; minimum = 2). This set of localities covered a latitudinal gradient extending from 55° N (northern Germany) to 37° N (Tunisia), and sampled the four genetic groups. Insular populations included the north Friesian islands (northern Germany), Atlantic and Mediterranean French islands including Corsica; Sardinia, Elba and Sicily (Italy), and finally, Ibiza (Spain).

The comparison with the Japanese wood mice included sixty-one specimens of *A. argenteus* (eight localities) and eighty-nine from *A. speciosus* (eight localities). The localities covered the latitudinal gradient on the main Japanese island Honshu, considered as a mainland situation, and five smaller islands (Renaud & Millien, 2001).

### Outline analysis

Mandible shape was quantified using outline analyses based on Fourier method. The outline corresponded to a two-dimensional projection of the mandible, put on its side with the lingual side down (Fig. 2). As the incisor was often free moving, and the molars sometimes missing, these features were not included in the study and only the outline of the mandibular bone was considered. The starting-point of the outline was defined at the meeting point of the incisor and the bone on the upper edge of the mandible. Only mature specimens with complete eruption of the third molar were considered. Mirror images of right mandibles were considered, to allow comparison with left ones. For each mandible, sixty-four points at equally spaced intervals along the outline

were sampled. Two Fourier methods were applied to this original data set.

Firstly, a radial Fourier transform (RFT) was applied. From the  $x$ ,  $y$  coordinates of the points, sixty-four radii corresponding to the distance of each point to the centre of gravity of the outline were calculated. A Fourier transform was then applied to this set of sixty-four radii. The outline is thus expressed as a finite sum of trigonometric functions of decreasing wavelength (harmonics) according to the formula:

$$r(s) = A_0 + \sum_{n=1}^K [A_n \cos(2\pi ns/L) + B_n \sin(2\pi ns/L)]$$

where  $r$  is the radius at the abscissa  $s$  along the outline,  $L$  the perimeter,  $K$  the number of points along the outline, and  $n$  the rank of the harmonic. The outline is therefore described by the set of Fourier coefficients  $A_n$  and  $B_n$ . The zeroth harmonic,  $A_0$ , is proportional to the size of each specimen and was used to standardize all the Fourier coefficients, in order to retain shape information only.

The second method corresponds to the Elliptic Fourier transform (EFT), performed using EFAwin (Ferson *et al.*, 1985). This method is based on the separate Fourier decompositions of the incremental changes of the  $x$ - and  $y$ -coordinates as a function of the cumulative length along the outline (Kuhl & Giardina, 1982). Any harmonic corresponds to four coefficients:  $A_n$  and  $B_n$  for  $x$ , and  $C_n$  and  $D_n$  for  $y$ , defining an ellipse in the  $xy$ -plane. The coefficients of the first harmonic, describing the best-fitting ellipse of any outline, are used to standardize the size and orientation of the object. These coefficients therefore correspond to residuals after standardization, and should not be included in following statistical analyses (Crampton, 1995).

In order to determine the rank of the last harmonic that has to be retained for a satisfactory description of the outline, two criteria can be considered: measurement error and information content. Measurement error is estimated here by ten repeated measurement of one randomly chosen specimen, and expressed as the coefficient of variation of the harmonic amplitude, i.e. the square root of the sum of the squared Fourier coefficients (Renaud *et al.*, 1996; Renaud & Millien, 2001). The content of information added by each harmonic is estimated using the cumulative power (Crampton, 1995). All results are congruent and indicate that the first seven harmonics offer a good compromise between measurement error and information content, for the RFT as well as the EFT (Fig. 3a, b). This similitude between the two methods underlines that the cut-off rank is determined by geometrical properties of the object, and that the EFT, computing four coefficients per harmonic, requires twice the number of variables of the RFT for attaining a similar description of the object.

From a set of Fourier coefficient, an outline can be reconstructed using an inverse method (Rohlf & Archie, 1984), providing a visualization of the shape changes involved. EFT method provides very accurate reconstructions because the inverse Fourier transform directly provides the euclidian  $xy$ -coordinates of the reconstructed outline

**Table 1** Localities composing the groups used in the statistical analyses, with latitude and number of mandibles analysed (Nb)

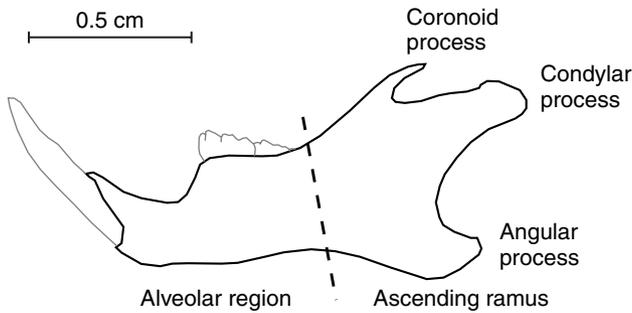
| Group  | M/I | Country     | Locality        | Coll  | Nb | Latitude |
|--------|-----|-------------|-----------------|-------|----|----------|
| D-N    | M   | Germany     | Plön            | IFH   | 11 | 54.2     |
|        |     |             | Preetz          | IFH   | 43 | 54.2     |
|        |     |             | Kiel            | IFH   | 22 | 54.3     |
| D-NF   | M   | Germany     | Nordfriesland   | IFH   | 10 | 54.6     |
| D-C    | M   | Germany     | Soest           | IFH   | 5  | 51.6     |
| D-AM   | I   | Germany     | Amrum           | IFH   | 21 | 54.7     |
| D-FO   | I   | Germany     | Föhr            | IFH   | 42 | 54.7     |
| D-SY   | I   | Germany     | Sylt            | IFH   | 26 | 54.9     |
| CH     | M   | Switzerland | Zurich          | JRM   | 2  | 47.4     |
| BE     | M   | Belgium     | Liege           | JRM   | 2  | 50.6     |
|        |     |             | Dalhem          | JRM   | 16 | 51.0     |
|        |     |             | St Méen         | MHNNH | 6  | 48.2     |
| FR-CH  | M   | France      | Lignièeres      | MHNNH | 11 | 46.8     |
| FR-LA  | M   | France      | Marais Poitevin | JRM   | 1  | 46.8     |
|        |     |             | Puceul          | MHNNH | 21 | 47.6     |
| FR-OL  | I   | France      | Oléron          | JRM   | 15 | 45.9     |
| FR-IW  | I   | France      | Ré              | JRM   | 6  | 46.2     |
|        |     |             | Yeu             | JRM   | 1  | 46.7     |
|        |     |             | Noirmoutier     | JRM   | 3  | 47.0     |
| FR-C   | M   | France      | Morvan          | JRM   | 9  | 47.3     |
| FR-MTP | M   | France      | Montpellier     | JRM   | 14 | 44.0     |
| FR-S   | M   | France      | Cap Lardier     | JRM   | 4  | 43.3     |
|        |     |             | Esterel         | JRM   | 1  | 43.4     |
|        |     |             | La Penne        | JRM   | 4  | 43.9     |
|        |     |             | Cévennes        | JRM   | 2  | 44.4     |
|        |     |             | Porquerolles    | JRM   | 8  | 43.0     |
| FR-IS  | I   | France      | Port Cros       | JRM   | 4  | 43.0     |
|        |     |             | Bonifacio       | JRM   | 3  | 41.4     |
| CO     | I   | France      | Fango           | JRM   | 5  | 42.4     |
|        |     |             | Gambaria        | JRM   | 3  | 38.2     |
| IT     | M   | Italy       | Tarquimia       | JRM   | 25 | 42.3     |
|        |     |             | Grosseto        | JRM   | 5  | 42.8     |
|        |     |             | Sardinia        | JRM   | 2  | 40.9     |
| IT-ES  | I   | Italy       | Elba            | JRM   | 1  | 42.8     |
|        |     |             | Ficuzza         | JRM   | 6  | 37.7     |
| SIC    | I   | Italy       | Grateri         | JRM   | 9  | 38.0     |
|        |     |             | Marettimo       | JRM   | 1  | 38.0     |
|        |     |             | Banyuls         | JRM   | 6  | 42.5     |
| PYR    | M   | France      | Banyuls         | JRM   | 6  | 42.5     |
|        |     | Spain       | Figueras        | JRM   | 5  | 42.3     |
| SP-MUR | M   | Spain       | Fabian          | JRM   | 4  | 42.6     |
|        |     | Spain       | Murcia          | JRM   | 15 | 38.0     |
| SP     | M   | Spain       | Alcoy           | JRM   | 10 | 38.7     |
|        |     |             | Trujilo         | JRM   | 2  | 39.5     |
|        |     |             | Nogais          | JRM   | 3  | 42.8     |
|        |     |             | Posada          | JRM   | 3  | 43.2     |
|        |     |             | Ibiza           | JRM   | 9  | 38.9     |
| PO     | M   | Portugal    | Murta           | JRM   | 3  | 39.0     |
| BU     | M   | Bulgaria    | Petric          | JRM   | 2  | 41.4     |
| TU     | M   | Tunisia     | Zaghouan        | JRM   | 3  | 36.3     |
|        |     |             | Aindram         | JRM   | 7  | 36.8     |

M/I: mainland/island; Coll: collection; IFH: Institut für Haustierkunde, Kiel, Germany; MHNNH: Museum National d'Histoire Naturelle, Paris, France; JRM: Johan R. Michaux.

(Fig. 3d). Less accurate reconstructions are obtained using RFT method, because  $xy$ -coordinates are calculated from the set of radii provided by the inverse Fourier transform (Fig. 3c).

### Statistical analysis

For each outline, different data sets have been considered: fourteen variables for the RFT considering seven harmonics



**Figure 2** Mandible of *Apodemus sylvaticus* in lateral view, with anatomical parts discussed in this study. Scale bar is 0.5 cm.

(RFT<sub>7</sub>), and twenty-four variables for the EFT considering seven harmonics (EFT<sub>7</sub>). In order to test if the reduction of the data set to the first seven harmonics did not lose information about morphological details of biological importance, another data set corresponding to the first sixteen EFT coefficients (EFT<sub>16</sub>) was finally considered.

Multivariate analysis of variance (MANOVA) were performed on these variables, in order to evaluate the importance of among-group differentiation relatively to within-group variations. This method allows limiting the effect of unbalanced sample size, and the influence of important local shape variation. The factors considered were localities (or groups of localities in the case of limited number of animals available), and were therefore independent of genetic, specific, or geographical designations. A test of significance for among-group differences (Wilk's Lambda test) is also provided. Associated with the MANOVA, canonical functions are estimated, the first of which are sufficient to account for the most important group differences (Marcus, 1993; Manly, 1994). In a first analysis, only specimens from *A. sylvaticus* were included. A second analysis included specimens of *A. sylvaticus*, *A. argenteus* and *A. speciosus*.

These analyses provided synthetic shape axes (canonical axes) that were compared with latitude using linear regression, considering average values per geographic groups, as well as all individuals separately. Furthermore, within *A. sylvaticus*, a multiple linear regression between latitude and the Fourier coefficients allowed for testing the existence of a latitudinal gradient independently of the canonical analysis.

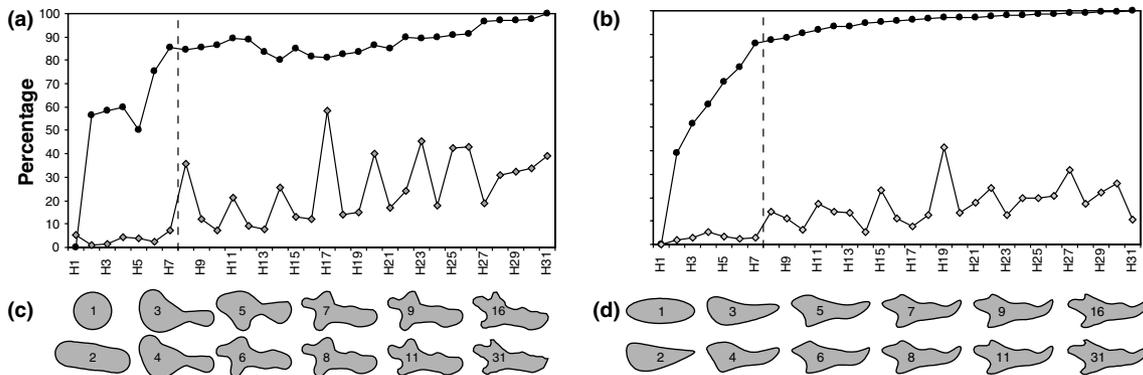
Finally, patterns of size variation were investigated within *A. sylvaticus*. The size estimator considered was the zeroth harmonic of the RFT outline analysis.

**RESULTS**

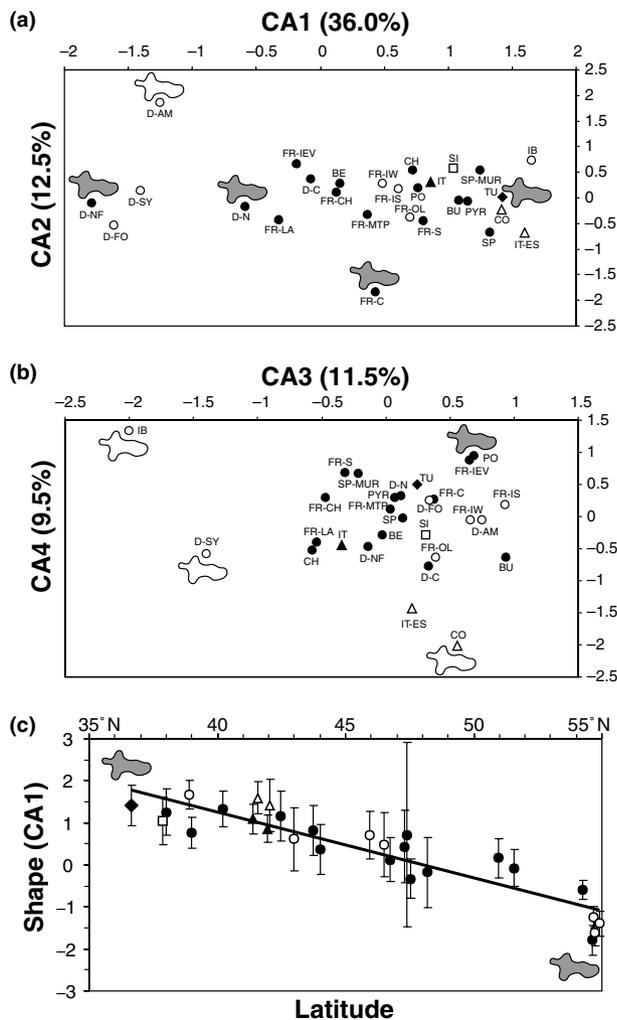
**Differentiation within the European wood mouse**

MANOVAS the different data sets (RFT<sub>7</sub>, EFT<sub>7</sub> and EFT<sub>16</sub>) indicated in all the cases that a morphological differentiation of the mandible outline exists among the European wood mouse ( $P < 0.0001$ ). Results of RFT<sub>7</sub>, providing the most efficient data reduction, are first presented in details.

Geographical groups are displayed along the first canonical axis (CA1, 36.0% of among-group variance) independently of their genetic origin or degree of isolation (Fig. 4). This shape gradient appears to be highly related to latitude ( $n = 28$ ,  $r^2 = 0.825$ ,  $P < 0.001$ ), and to correspond to reduced coronoid and angular processes towards the northernmost populations. It might correspond mainly to a gradient within the north-western genetic group, as the reduced latitudinal coverage within the other groups limits any interpretation. The next axes displayed rather local differentiation than global signals, involving mainly insular wood mice from the island of Amrum (northern Germany) on CA2 (12.5%), islands of Sylt (northern Germany) and Ibiza (Spain) on CA3 (11.5%), and islands of Corsica (France), Elba and Sardinia (Italy) on CA4 (9.5%). These cases of insular divergence involve various morphological features, such as



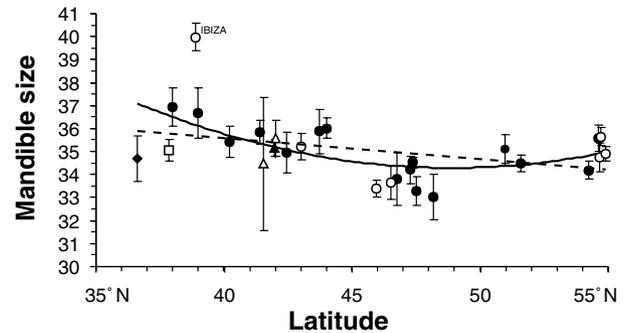
**Figure 3** Measurement error (grey diamonds) and cumulative power (black dots) as a function of the harmonic order for the radial Fourier transform (a) and the Elliptic Fourier Transform (b), and corresponding examples of reconstructed outlines for an increasing number of harmonics (c, d). The measurement error is expressed as the coefficient of variation of the harmonic amplitude of one specimen measured ten times. Cumulative power corresponds to the deviation of reconstructed outlines based on an increasing number of harmonics from the reconstruction based on the maximum number of harmonics (31).



**Figure 4** Morphological differentiation of the mandible within the European wood mouse [calculated on coefficients of the radial Fourier transform (RFT<sub>7</sub>)]. (a) Shape differentiation on the first two canonical axes. (b) Idem, on the third and fourth canonical axes. (c) Latitudinal shape gradient within the European wood mouse (*Apodemus sylvaticus*). The first multivariate axis is considered as a synthetic shape axis. Full line corresponds to the regression of shape (CA1) with latitude. Symbols as in Fig. 1a; labels in Table 1. Reconstructed outlines exemplify the shape variation and correspond to the mean values of some localities (grey, from mainland; open, from islands).

a wider mandible in Ibiza, and a more pronounced coronoid process in Amrum.

The main morphological differentiation on CA1 is not the consequence of an allometric relationship between size and shape of the mandible, as these variables are not significantly correlated ( $n = 28$ ,  $r^2 = 0.087$ ,  $P < 0.128$ ). Mandible size does not display obvious differences among genetic groups (Fig. 5). Overall, a weak trend towards decreasing size with higher latitudes is observed, but the linear model only poorly fitted the data ( $n = 28$ ,  $r^2 = 0.152$ ,  $P = 0.040$ ) whereas a



**Figure 5** Latitudinal size variations within the European wood mouse (*Apodemus sylvaticus*). The size of the mandible was estimated based on the outline analysis as the zeroth harmonic amplitude of the RFT. Dotted line: linear regression; full line: second order polynomial regression. Symbols as in Fig. 1a.

better correlation is obtained by a second order polynomial regression ( $r^2 = 0.321$ ). Size might, therefore, be characterized by nonlinear variations with minimal sizes at intermediate latitudes. Additionally, the expected insular gigantism does not emerge clearly over this large-scale geographical sampling, except in the case of Ibiza population, obviously larger than mainland populations from similar latitudes (Fig. 5).

#### Comparison of the Fourier methods

In order to test the different methods of outline analysis, the patterns of morphological variation within the European wood mouse based on the various data sets (RFT<sub>7</sub>, EFT<sub>7</sub> and EFT<sub>16</sub>) were compared. In all the cases, MANOVA were significant, but the higher the number of variables (fourteen for RFT<sub>7</sub>, twenty-four for EFT<sub>7</sub>, sixty for EFT<sub>16</sub>), the more the variance explained is diffuse among the successive axes (Table 2). However, the pattern expressed by CA1s are highly correlated ( $P < 0.001$ ). The correlation between CA2s is not as good ( $P < 0.01$ ), mainly because a more important divergence of the Ibiza population in the EFT<sub>16</sub> analysis.

The patterns of morphological differentiation as a function of latitude emerge in a very similar way with all the three Fourier methods, both considering a multiple linear regression of the Fourier coefficients against latitude, and a linear regression of CA1 with latitude (Table 2). These results show that the data reduction from a high number of harmonics to seven, suggested by measurement error and cumulative power (Fig. 3), adequately describes the characters involved in the morphological differentiation of the mandible, although subtle details of the articular processes are involved. Furthermore, the RFT appears to describe the morphological differentiation with fourteen variables as efficiently as the EFT with twenty-four variables, although graphical reconstructions are not as good. Therefore, the subsequent analyses involving a reduced numbers of specimens, the RFT<sub>7</sub> was preferred because providing the most

**Table 2** Comparison of the Fourier methods for the analysis of the intraspecific variation of *Apodemus sylvaticus*. *n*: number of individuals (*n* = 442: all specimens; *n* = 28: group means)

|   | RTF <sub>7</sub> | EFT <sub>7</sub> | EFT <sub>16</sub> |
|---|------------------|------------------|-------------------|
| MANOVA  | ***              | ***              | ***               |
| CA1 (% var) ( <i>n</i> = 442)                                 | 35.6             | 33.1             | 31.1              |
| CA2 (% var) ( <i>n</i> = 442)                                 | 12.7             | 9.8              | 8.8               |
| CA3 (% var) ( <i>n</i> = 442)                                 | 11.9             | 8.3              | 7.7               |
| Correlation between canonical axes                            |                  |                  |                   |
| CA1   |                  |                  |                   |
| EFT <sub>7</sub>  | 0.920***         |                  |                   |
| EFT <sub>16</sub>   | 0.911***         | 0.976***         |                   |
| CA2   |                  |                  |                   |
| EFT <sub>7</sub>  | 0.906***         |                  |                   |
| EFT <sub>16</sub>   | 0.529**          | 0.535**          |                   |
| Multiple linear regression, latitude vs. Fourier coefficients |                  |                  |                   |
| <i>R</i> ( <i>n</i> = 442)                                    | 0.682***         | 0.741***         | 0.815***          |
| Linear regression, CA1 vs. latitude                           |                  |                  |                   |
| <i>R</i> ( <i>n</i> = 28)                                     | 0.910***         | 0.860***         | 0.858***          |
| <i>R</i> ( <i>n</i> = 442)                                    | 0.675***         | 0.723***         | 0.723***          |

\*\*\**P* < 0.01; \*\**P* < 0.001.

efficient data reduction. Average reconstructed outlines based on EFT<sub>16</sub> were nevertheless obtained for support to a visual interpretation.

**Comparison among species of wood mice**

In order to test the generality of the latitudinal shape gradient, the morphological pattern observed in the European wood mouse *A. sylvaticus* was compared with that in two other species of wood mice, *A. argenteus* and *A. speciosus* (Fig. 6). Shape differentiation was highly significant (Wilk’s Lambda test: *P* < 0.0001). The first order signal emerging from the morphometric analysis of the mandible was associated with interspecific differentiation. The first axis (CA1, 42.2% of among-group variance) separated *A. sylvaticus* from *A. speciosus* while the second axis (CA2, 21.3%) segregated *A. argenteus* from the latter (Fig. 6a). However, the third axis (CA3, 11.7%) displayed intraspecific patterns of variation, corresponding again to a latitudinal trend (Fig. 6b). The latitudinal shape gradient was similar for all three species (Table 3), although less clear in the case of *A. argenteus*. The latitudinal mandible shape changes involve a south–north flattening of the articular processes in the three species, a shape change visualized by outline reconstruction of the northermost and southernmost geographical groups for each species.

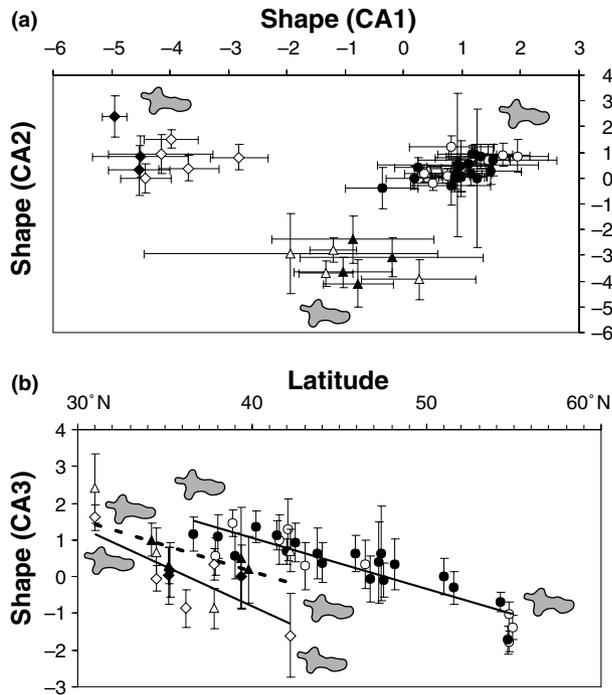
**DISCUSSION**

**Genetic constraints on mandible shape and its response to selection**

A number of studies about the genetic architecture of the rodent mandible provide a theoretical framework for understanding how the mandible can be affected by drift or

founder effects, or how it can respond to selection. Developmental and genetic evidences suggest that the mandible consists of two relatively independent modules (Atchley *et al.*, 1992; Mezey *et al.*, 2000), the anterior part of the mandible, or alveolar region, bearing the incisor and molars, and the posterior part of the mandible, or ascending ramus, corresponding to the zone of muscular insertion with the muscular processes (Fig. 2). This suggests that these two modules, being subjected to different evolutionary pressures, could evolve relatively independently. Furthermore, quantitative genetics analyses suggested that the rodent mandible shape was controlled by multiple genes with a reduced effect generally localized in specific regions of the mandible, such as the muscular processes of the ascending ramus (Cheverud *et al.*, 1997). Several loci can affect similar shape features, suggesting that some traits could respond more easily to selection. Among them emerge as a recurrent pattern a dorso-ventral expansion or compression of the mandible, combined with weaker anterior–posterior shifts of the coronoid and angular processes (Klingenberg *et al.*, 2001; Klingenberg & Leamy, 2001). Developmental and genetic constraints would thus channel variations of diverse origins to be expressed in such recurrent phenotypic patterns, making them prone to a maximal response to selection (Klingenberg & Leamy, 2001).

In this framework, comparing the shape features involved in the differentiation of the wood mice provides contrasted results (Fig. 7). Interspecific differences (Fig. 7a) involve traits on the whole mandible. This could be interpreted as the consequence of the high numbers of genes involved, and possible pleiotropic, non-adaptive effects of the interspecific divergence leading to this general shape differentiation. Differently, insular (Fig. 7b) and latitudinal differentiation (Fig. 7c) correspond to more localized shape variations that will be discussed thereafter.



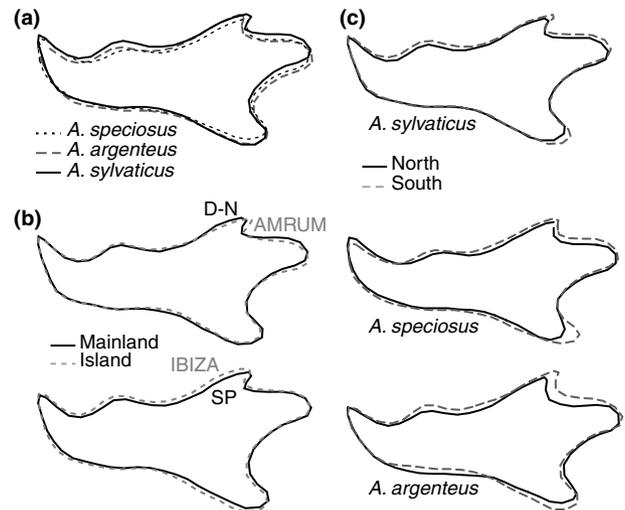
**Figure 6** Inter- and intraspecific patterns of variations in three species of *Apodemus* [calculated on coefficients of the radial Fourier transform (RTF<sub>7</sub>)]. (a) Interspecific differences on the two first multivariate axes (CA1, 42%; CA2, 21%). Populations included *A. sylvaticus* (circles), *A. argenteus* (triangles), *A. speciosus* (diamonds) animals as well as mainland (close symbols) and island (open symbols). (b) Intraspecific variation expressed on the third axis (CA3, 12%) as a function of latitude. Lines correspond to linear regression of shape (estimated by mean scores on CA3) as a function of latitude for the three species of wood mice (full lines:  $P < 0.05$ ) dotted line:  $P < 0.10$ ). Average outlines corresponding to each species (a) and southernmost and northernmost locality for each species (b) allow visualization of shape differences.

**Table 3** Relationship between intraspecific shape variation (estimated by mean score of the geographical groups on CA3, calculated on RTF<sub>7</sub> coefficients) and latitude. Results of linear regression analyses are provided: coefficient of correlation ( $R$ ), probability ( $P$ ), and slope  $\pm$  SE

|                                    | $R$   | $P$     | Slope  | $\pm$ SE |
|------------------------------------|-------|---------|--------|----------|
| <i>A. sylvaticus</i> ( $n = 442$ ) | 0.639 | < 0.001 | -0.142 | 0.008    |
| <i>A. argenteus</i> ( $n = 61$ )   | 0.276 | 0.030   | -0.100 | 0.045    |
| <i>A. speciosus</i> ( $n = 89$ )   | 0.517 | < 0.001 | -0.217 | 0.039    |
| Regression on group means          |       |         |        |          |
| <i>A. sylvaticus</i> ( $n = 28$ )  | 0.889 | < 0.001 | -0.139 | 0.014    |
| <i>A. argenteus</i> ( $n = 8$ )    | 0.633 | 0.092   | -0.158 | 0.079    |
| <i>A. speciosus</i> ( $n = 8$ )    | 0.791 | 0.020   | -0.218 | 0.068    |

### Impact of insularity on size and shape

Insular syndrome in rodents has been characterized especially by a tendency towards gigantism, an effect particularly



**Figure 7** Comparison of reconstructed outlines (calculated on the coefficients of the first sixteen harmonics for the Elliptic Fourier Transform EFT<sub>16</sub>). (a) Interspecific differences. (b) Examples of insular divergence within *Apodemus sylvaticus*: average mandible shape of the specimens from the North Friesian island of Amrum compared with the Northern Germany group (D-N), idem for average shape from Ibiza compared with the Spanish group (SP). (c) Latitudinal mandible shape difference within the three species of wood mice. The northernmost locality is compared to the southernmost one.

enhanced on small islands. The size of the lower incisor is related to body size in rodents (Millien-Parra, 2000), and it is likely that the whole mandible is similarly related to body size. It can, therefore, be considered as an estimator of this latter variable. At the exception of the specimens from Ibiza, obviously larger than the Spanish mainland ones, no clear trend towards larger mice on island emerge from our results (Fig. 5). Hence, the present study brings few support to the insular gigantism, although it has been previously described in the European wood mouse (Angerbjörn, 1986; Michaux *et al.*, 2002b). This result is in agreement with those of a previous study on the Asiatic wood mice *A. argenteus* and *A. speciosus*, where size only provided limited response to insularity (Renaud & Millien, 2001). It might be the case that a trend towards larger size in islands can only be highlighted by a local study focused on the insular populations and their nearest mainland relatives. Alternatively, insular gigantism might develop only in some particular cases combining a small area of the island and a depleted predator fauna (Michaux *et al.*, 1996b, 2002b), as in the case of Ibiza.

Morphological divergence of small mammals insular populations have already been observed (Berry, 1969, 1973), especially on North Friesian island populations of *A. sylvaticus* (Murbach, 1979) included in the present study, and Asiatic wood mice *A. argenteus* and *A. speciosus* (Renaud & Millien, 2001). In agreement with these previous studies, our analysis evidence a random shape differentiation

on some islands, i.e. Amrum, Sylt, Ibiza, Corsica, Elba and Sardinia. It can be depicted as a pattern of variation with mainland populations in a central position, from which the insular populations diverge randomly in various directions (Fig. 4). Various parts of the mandible are involved in the insular divergence, indicating that this is not the consequence of an adaptation to specific insular conditions. Noteworthy, the important differentiation of the Amrum population reported based on skull characters (Murbach, 1979) is also evidenced by our analysis on the mandible shape. It differentiates from the mainland populations by an elongation of the coronoid process (Fig. 7b). Differently, the population of Ibiza differentiates from its mainland counterpart by a more global dorso-ventral expansion (widening) of the mandible.

The differentiation of island populations may have a genetic basis and be interpreted as the combined result of a founder effect, and subsequent genetic drift, because of reduced gene flow through isolation. However, genetic analyses poorly support this idea, as no important genetic differentiation of island populations of *A. sylvaticus* has been recorded (Michaux *et al.*, 1996a, 1998a, 2002b). Alternatively, important local morphological differentiation has been reported in the house mouse (Auffray *et al.*, 1996) and such random effect may be enhanced on islands.

The very localized difference of the Amrum population suggests that few genes are involved; the more important differentiation of the population from Ibiza matches one of the recurrent pattern produced by a variety of loci (Klingenberg & Leamy, 2001). Both observations suggest that the random insular differentiation observed on the mandible shape is not in contradiction with the limited amount of genetic differentiation recorded.

#### Intraspecific size variations in the wood mouse

Size has been a morphological character more widely investigated than shape, mainly because it is more easily quantified. Thus, various patterns of size variations have been recognized, as gigantism of insular rodent populations (Foster, 1964; Lomolino, 1985; Michaux *et al.*, 2002b), and the trend towards an increase in size with latitude, or Bergmann's rule (Bergmann, 1847; Mayr, 1942). The present study poorly supports the insular gigantism, and provides no evidence for the expected increase in size towards high latitude. Rather, a trend towards decreasing size in colder environment is observed, although the size variations do not occur linearly with latitude (Fig. 5), in agreement with previous observations across French populations (St Girons, 1966). A similar feature of increasing size with increasing temperature has also been observed within the Asiatic wood mouse *A. argenteus* (Renaud & Millien, 2001). These results confirm that wood mice do not vary in size according to the Bergmann's rule, but rather according to an inverse pattern. Yet, the nonlinear size variations observed within the European wood mouse might result of competing effects of different factors, leading to a minimum size around 45–47° N of latitude. The slight increase in size from 45 to

55° N might thus be because of a Bergmann's effect in northernmost environments.

#### Adaptive significance of the latitudinal shape gradient

The random differentiation associated with insularity was observed in the Asiatic wood mice to compete with an alternative cause of shape differentiation, namely geographical gradients (Renaud & Millien, 2001). Both species displayed a similar response in shape to the environmental gradient covered by the Japanese archipelago. This result is strongly corroborated by the patterns emerging from the present study. A latitudinal shape gradient is found independently in the European wood mouse *A. sylvaticus*, emerging as the first order signal of the shape differentiation on our large scale study (Fig. 2). Additionally, when the three species are compared within a single analysis (Fig. 4), intraspecific shape gradients appear to be similar, corresponding to a dorso-ventral expansion of the mandible, with more divergent coronoid and angular processes, towards the south. Such a shape feature once again matches one of the morphological patterns identified as able to easily respond to selection (Klingenberg & Leamy, 2001). The expression of this phenotypic pattern as a similar latitudinal gradient in the three species of *Apodemus* suggests that it constitutes in this case a response to a common selective pressure acting on mandible shape. Yet, a functional analysis of such subtle shape variations is difficult. Studies on interspecific differences in rodents have nevertheless shown that coronoid and angular processes are zones of attachment of the muscles involved in biting and mastication, whereas the condylar process plays a pivotal role in the articulation with the skull (Kesner, 1980; Satoh, 1997). The hypothesis of a relationship between latitudinal trends in ecology, especially feeding behaviour, and differential development of muscles causing changes in the mandible shape can therefore be proposed.

Comparisons of mandible morphology among related genera supports such an interpretation. In closely related phylogenetic groups such as *Rattus* and *Bandicota* (Verneau *et al.*, 1998), a flattened mandible shape in *Rattus* is associated with a basic dental pattern and an omnivorous–granivorous diet whereas a higher mandible in *Bandicota* is found together with hypsodont teeth, suggestive of a herbivorous diet (Marshall, 1988). As the latter diet is more abrasive, it requires more efficient mastication (Michaux, 1978). A parallel change towards a wide mandible is found in the African rodent *Otomys* (Taylor & Kumirai, 2001), associated with extremely specialized molars allowing for grass eating.

#### Possible relationship between mandible shape and ecology

The European wood mouse is mainly granivore, but its feeding behaviour may vary according to environmental factors. Firstly, the wood mouse can adjust its diet as a function of the vegetation cover. It feeds essentially on seeds in deciduous woodlands but can compensate a limited seed availability through an increased uptake of other food

resources, such as animal food and plant material in environments such as coniferous plantations and sand-dunes (Butet, 1986; Montgomery & Montgomery, 1990; Butet, 1994; Rogers & Gorman, 1995). Secondly, the wood mouse adjusts its diet according to the season. Seed uptake is usually minimum in spring, between the exhaustion of autumn tree seed crop and seed production by herbs in summer (Montgomery & Montgomery, 1990; Montgomery *et al.*, 1991). Shifts in feeding behaviour might further be related to metabolic requirements, with a trade-off between high energy value of the ingested food during winter, and protein contents during the breeding period (Butet, 1990, 1994).

The intergeneric comparison between mandible shapes suggests that the latitudinal change in morphology observed within the wood mice may be related to change in diet. Firstly, variations in habitat might be invoked. However, this hypothesis does not properly explain a latitudinal gradient, as the wood mouse appears to be most successful in deciduous woodlands (Attuquayefio *et al.*, 1986; Montgomery & Montgomery, 1990) and this habitat is present over a wide range of latitude, being present in Europe up to Scandinavia. Optimal habitats for wood mice therefore exist all over the investigated gradient. Alternatively, winter season increases in duration and intensity with latitude, therefore a latitudinal trend in mean diet and ecology is expected. On average wood mice in high latitudes should confront a longer period of limited grain availability in winter, before summer seed production. During this extended intermediate period, wood mice should diversify their feeding behaviour in order to maintain its high-energy value. The dorso-ventrally compressed mandible observed in high latitude *Apodemus* populations might, therefore, be related to an omnivorous diet, a trend also observed in *Rattus*.

Additional factors may also play a role, e.g. social behaviour. Further seasonal variations in behaviour are observed, such as increase of males home range in late spring, in relation with the mate seeking activity (Randolph, 1977; Attuquayefio *et al.*, 1986; Montgomery *et al.*, 1991). This behaviour is coupled with a development of territoriality and increased aggressivity in males during the breeding season, whereas overwintering wood mice are friendly with other individuals (Randolph, 1977). Because of varying relative length of the seasons with latitude, differences in average levels of aggressivity might exist. It has been recently suggested that morphological differences in rodent skull could be related to levels of aggressivity (Corti & Rohlf, 2001). Several ecological factors might, therefore, be combined in underlying the observed latitudinal trend in mandible shape.

#### Timing of the latitudinal differentiation

As *A. sylvaticus* recolonized Northern Europe after the last glaciation from an Iberic refuge zone (Michaux *et al.*, 2002a), the formation of such a latitudinal gradient appears to have been rapid, in the order of 16,000 years. Such a rapid response to selection might be possible through the existence of developmental and genetic pathways favouring

the response to selection of certain shape features. This result is of importance for palaeontological studies, where genetic data are not available. Rather than reflecting fine-scale genetic heterogeneity, shape appears to mirror large-scale environmental patterns, and palaeoenvironmental interpretation of these variations should not be misleading.

## CONCLUSIONS

Based on a morphometrical analysis of the mandible, the factors patterning shape differentiation within the European wood mouse *A. sylvaticus* have been investigated. Genetic structure is known in this species but appears to have little influence on morphology. Insular effects can be recognized, especially a random morphological differentiation of some islands populations. However, the best known effect of the insular syndrome, e.g. a trend of rodents towards gigantism on islands, is poorly supported. Surprisingly, the most important factor in patterning mandible shape appears to be latitude. A comparison with two Asiatic species of wood mice, *A. argentatus* and *A. speciosus*, evidences that a similar morphological gradient evolved several times independently, in a relatively short time span. This suggests an adaptive significance of these mandible shape variations. Mandible is involved in the feeding process, and changes in its shape might be related to changes in masticatory efficiency. The ecology, and especially the feeding behaviour, of the wood mice are known to change seasonally. As the relative importance of the seasons varies with latitude, latitudinal mandible shape variations might be a response to a change in the average annual diet and behaviour.

## ACKNOWLEDGMENTS

We thank N. Taylor, J. Britton-Davidian, J. Michaux, R. Libois, J. Cassaing, P. Chevret and C. Girard for comments on the manuscript. We are indebted to D. Kruska for access to the collection of IFH (Kiel, Germany), R. Lucht for technical help during measurement at IFH, and to C. Denys at the MNHN (Paris, France). The remarks of C.P. Klingenberg and one anonymous reviewer significantly improved the manuscript. This research was supported by the French IFB, GDR 2474 CNRS, Rhône-Alpes region, and Belgian FNRS.

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