



ORIGINAL INVESTIGATION

Seasonal variation in molar outline of bank voles: An effect of wear?

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Received 8 January 2009; accepted 19 March 2009

Abstract

Morphometric characters can be of use for elucidating the evolutionary history of species by providing an insight into the selective pressure related to the character of interest, and by allowing integration of fossil specimens. This potential interest of phenotypic characters, however, depends on how much other sources of variation, such as the life-history of the animal, may blur an evolutionary signal. For instance, age structure varies along the year, causing in turn various assemblages of wear stages in the teeth sampled at a given place and time. In this context, we investigated the season of trapping as potential source of variation in the size and shape of the molar occlusal surface of the bank vole, *Clethrionomys glareolus*.

The size and shape of the occlusal surface of the third upper molar was quantified using outline analysis in 60 bank voles from Finland, trapped at the same study site in successive spring and autumn. The occlusal surface clearly differed in size and shape between the two seasons of trapping. Using 3D imaging as a visual support, we interpret this difference as the result of differential wear. The population in autumn is dominated by young specimens with unworn teeth whereas spring populations are composed of old animals with worn down molars. The range of seasonal variation in tooth size and shape appears to be of the same order of magnitude as biogeographic variation, demonstrating that differential wear may have a strong impact on biogeographic and evolutionary studies. Yet, beyond the effect of trapping season, a biogeographic signal still emerged, related to the genetic lineages evidenced in other studies. In consequence, morphometric characters such as size and shape of molar occlusal surfaces appear as valuable tracers of biogeographic differentiation, but future studies should take seasonal variations into account for more robust interpretation.

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Keywords: Morphometrics; Rodentia; Arvicolinae; *Myodes*; Biogeography

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Introduction

Bank voles (*Clethrionomys* [proposed to be renamed as *Myodes*; Wilson and Reeder, 2005; however, this change being so far not widely established we kept the former name in the subsequent text] *glareolus*; Arvicolinae, Rodentia) are forest rodents present in all Europe, extending eastwards as far as Siberia. Genetic studies based on mitochondrial DNA showed the existence of several phylogeographic groups (Deffontaine et al. 2005) including Mediterranean lineages (Italy and Spain), and several lineages in central, western and northern Europe (Fig. 1). The differentiation of these phylogroups is the consequence of successive fragmentation of their habitats during glacial cycles, leading to repeated isolation of populations in various refugia (Deffontaine et al. 2005; Kotlík et al. 2006). Among these lineages, the Ural group is characterised by a mitochondrial DNA (mtDNA) similar to the mtDNA of the congeneric vole species, the red vole *Clethrionomys rutilus* (Fig. 1B) despite a *glareolus* nuclear DNA

(Tegelström 1987; Deffontaine et al. 2005). The occurrence of a *rutilus* mtDNA within a *glareolus* lineage has been attributed to an introgression of red vole mtDNA into bank vole, probably due to a hybridization event (Tegelström 1987; Deffontaine et al. 2005; Potapov et al. 2007).

The differentiation of these lineages occurred during the Pleistocene glacial cycles and molecular clock analyses estimate the time of this divergence as ~300 000 yrs. This is recent regarding the geological time scale. Ongoing morphometric studies nevertheless suggest that this phylogeographic differentiation may already have led to significant phenotypic expression on the occlusal shape of upper molars (Ledevin et al. 2007). Such a result is promising for integrating paleontological data into phylogeographic studies, since teeth are the best conserved material in fossil deposits for small mammals such as voles. Another striking feature of these analyses, however, was the importance of the within-lineage variation. This raised the question of the source of such a variability interfering with the signal of phylogeographic differentiation.

Phylogeographic studies are based on samples trapped at various periods over the distribution area of the species, each locality being usually sampled once at a given date depending on trapping campaigns. Hence, seasonal and interannual variations in the population structure might underlie the important within-lineage variation observed on the third upper molar occlusal shape. As a first step to assess the sources of phenotypic variation, we focused on differences that may occur depending on the season of trapping and hence, on the age of the voles. First, differential reproduction success during summer and/or survival during harsh winter periods may constitute selective events shifting the composition of the population. Second, the age structure of the populations changes through the year, due to the seasonal reproduction periods (Tkadlec and Zejda 1998). In northern bank voles, breeding lasts from spring to autumn; hence animals trapped in spring are old, overwintered animals whereas trapping in autumn samples a variety of age classes, from relatively old to young animals born in summer.

Teeth get worn with the increasing age of the animal. The associated shape change of the 2D crown outline has been shown to be limited to old age classes in the wood mouse (Renaud 2005). However, wood mice are characterized by low-crowned molars, whereas voles display high-crowned, hypsodont teeth (Tesakov 1996). Many voles even display ever-growing teeth, although *Clethrionomys* presents an intermediate stage: molars are first unrooted at the beginning of the post-natal ontogeny, with subsequent apparition of oral and aboral roots that will grow all along the life of the animal (Lowe 1971). It seems that wear, and hence indirectly

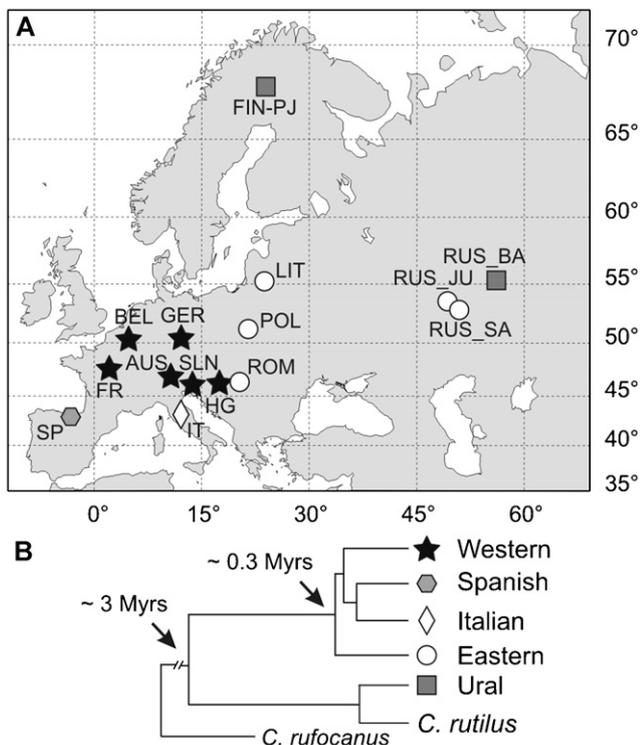


Fig. 1. Geographic sampling and phylogeographic background in bank voles. (A) Geographic localization and lineage attribution of the bank voles considered in the present study. The FIN_PJ locality corresponds to the studied area (Pallasjärvi, Finland). (B) Simplified tree representing the relationships among the Western, Eastern and Ural lineages, based on a neighbour-joining analysis of mtDNA haplotypes. Note that the Ural mtDNA is similar to the mtDNA of *Clethrionomys rutilus*. (after Deffontaine et al. 2005).

age, may affect the shape of the occlusal surface in bank voles (Borodin et al. 2006), and such an effect has been further proven to be of significant importance in some hypsodont mammals (Bair 2007).

As a first attempt to evaluate the occurrence of morphological difference in M3 occlusal shape due to season of trapping, samples composed of animals trapped at three successive time periods (spring 2000, spring 2001 and autumn 2001) in the same locality (Pallasjärvi, Finland) were considered. Using 2D outline analysis, the size and shape of the occlusal surface were quantified and compared among these samples. Finally, to evaluate how much such difference might interfere with geographic patterns, the amount of morphological variance caused by seasonal differences was compared with the range of phylogeographic variation (Ledevin et al. 2007).

Material and methods

Material

Bank voles were snap-trapped at Pallasjärvi, Finland (Fig. 1A), at three different periods: spring 2000, spring 2001 and autumn 2001. Sex was known for all spring animals. Autumn animals were non-breeding sub-adults for which sexual differences should not appear. Heads were preserved in 95%-ethanol and manually cleaned before the morphometric analysis. 20 individuals from

each group were analysed (10 males and 10 females when the sex was known).

In order to compare the seasonal variation of morphology with the phylogeographic signal, these animals were compared with bank voles from different European localities sampling most of the known lineages (Table 1; Fig. 1A), including a further sample from Pallasjärvi (12 specimens from autumn 2001). Bank voles at Pallasjärvi belong to Ural mtDNA clade, and the contact zone with the Eastern lineage in Finland and Western lineage in Sweden is more than 400 km south from Pallasjärvi.

All adult and sub-adult animals with completely erupted third molar were considered.

Data acquisition

Two kinds of morphometric analyses can be used to compare tooth shape: landmark-based methods and outline analysis. In bank voles, most landmarks would correspond to maxima and minima of curvature, whereas the outline of the occlusal surface efficiently describes the complex shape composed of neighbouring triangles (Navarro et al. 2004). For this analysis, the occlusal surface of the left third upper molar (M3), or a mirrored image of the right M3 if the left molar was damaged, was considered for each animal. The 2D outline of the occlusal surface was digitized as the external outline of the enamel ridge delimiting the crown. This 2D outline provided a good description of the occlusal surface of the molar since it was nearly flat

Table 1. Groups considered for seasonal differences at Pallasjärvi (Season) and geographic variations (Geography), with the number of specimens measured for the M3 occlusal surface (Nb.).

	Label	Country	Locality	Lineage	Nb.
Season	Spring 00	Finland	Pallasjärvi	Ural	10 ♀ + 10 ♂
	Spring 01	Finland	Pallasjärvi	Ural	10 ♀ + 10 ♂
	Autumn 01	Finland	Pallasjärvi	Ural	20
Geography	LIT	Lithuania	Alytus	East	4
	POL	Poland	Lublin	East	8
	ROM	Romania	Sovata	East	9
	RUS_JU (1)	Russia	Zhiguli mountains	East	4
	RUS_SA (2)	Russia	Ozerki	East	8
	RUS_BA	Russia	Bashkiria	Ural	25
	FIN_PJ	Finland	Pallasjärvi	Ural	12
	IT	Italy	Tuscany	Italy	10
	SP	Spain	Asturias	Spain	12
	AUS	Austria	Pfunds, Ventetal, Zemmtal	West	16
	BEL	Belgium	Blégne, Dalhem, Liège, Virelles	West	24
	FR	France	Loiret	West	2
	GER	Germany	Langenberg	West	3
	HG	Hungary	Bak	West	4
SLN	Slovenia	Delnice, Livek	West	3	

“Label” indicates the abbreviation used on the Figures; country and locality of trapping are mentioned as well as the phylogeographic lineage the specimens belong to.

in bank voles. A drawback is that the occlusal surface is directly affected by wear along the life of the animal. Unfortunately the vertical sides of the Arvicoline tooth prevent focusing at the base of the crown, a procedure that allows limiting the effect of wear in morphometric analyses of murine teeth (Renaud 2005).

The starting point was defined at the minimum between the first and the second anterior labial triangles. The OPTIMAS software (version 6.5) was used to extract the area enclosed by the outline, considered as an estimate of the tooth size, and the coordinates of 64 points at equal curvilinear distance on the outline.

Outline analyses

In order to quantify the shape of the molar, the 64 points along the outline were analysed by an Elliptic Fourier Transform (EFT), using the EFAwin software (Ferson et al. 1985). Such an analysis has been shown to efficiently describe variation in molar shape of Arvicoline rodents (Navarro et al. 2004).

Using this method, the outline is approximated by a sum of trigonometric functions of decreasing wavelength, the harmonics. Each harmonic is weighted by 4 coefficients A_n , B_n , C_n , D_n , and corresponds to an ellipse in the x,y plane. The first ellipse (defined by the coefficients A_1 , B_1 , C_1 , and D_1) contains information about the size, position and rotation of the molar, and has been used to standardize the outline data. Hence, the first three coefficients were not retained for the statistical analysis, as they correspond to residuals after standardization (Crampton 1995; Renaud et al. 1996). The fourth one, D_1 , corresponding to the minor axis of the ellipse, contains information about the elongation of the molar and was conserved in the analysis (Michaux et al. 2007).

Two different criteria are important to determine the rank of the last harmonic to be considered: the measurement error and the information content of each harmonic. A study on Arvicoline teeth suggested retaining 10 harmonics (Marcolini 2006).

In order to visualize the morphological changes between groups, average Fourier coefficients for each group were calculated, and the corresponding outline was reconstructed using an inverse Fourier method (Rohlf and Archie 1984) and the NTSYS software.

Statistical analyses

The differences in molar area between groups were tested by an analysis of variance (ANOVA). The shape of each molar was described by 37 Fourier coefficients (the last coefficient of the first harmonic, and 4 coefficients for each of the 9 subsequent harmonics). The difference in molar shape between seasonal groups

was tested by a MANOVA performed on the Fourier coefficients, and the associated Wilks' Lambda test.

The main patterns of shape variation among the three Pallasjärvi samples were expressed on synthetic shape axes obtained by a principal component analysis (PCA) on the Fourier coefficients. A PCA can be computed based on two different matrices: correlation or variance-covariance matrix. The analysis of the correlation matrix was used here because it is more sensitive to localized changes in the outline, as the Fourier coefficients are weighted for the analysis. A PCA on the variance-covariance matrix would have given more importance to the information of the first harmonics and to global shape differences (Michaux et al. 2007).

To further evaluate the importance of the seasonal differences compared with geographic differentiation, a PCA including both the seasonal samples from Pallasjärvi and the localities documenting geographic variation was performed. The existence of differences among lineages on the principal axes was tested by ANOVA on the principal scores.

Statistical analyses were performed using SYSTAT v.11 software and the R software ({R Development Core Team} 2008).

3D imaging

In order to further investigate the impact of progressive wear on the shape of the M3 occlusal surface, 3D images of the molar row were acquired for one specimen showing limited wear (PJS01-34, trapped in spring 2001). Data acquisition was performed using a μ CT-scanner, with slices spaced from 20 μ m and a final pixel size of 45 μ m (tomography performed by Voxcan, Lyon, France). Based on the 3D reconstruction, successive slices of the upper molar row were performed parallel to the occlusal surface, providing a visual approximation of the effect of progressive wear on the 2D shape of the occlusal surface.

Results

Influence of the trapping season on the size of the M3 occlusal surface

A possible sexual dimorphism of the molar area was tested and showed no difference between males and females in the pooled sample of springs 2000 and 2001 (ANOVA: $P = 0.964$), allowing to pool males and females together for subsequent analyses.

A significant difference in molar size between the three trapping seasons at Pallasjärvi was evidenced (ANOVA: $P < 0.001$). Animals trapped in spring 2000

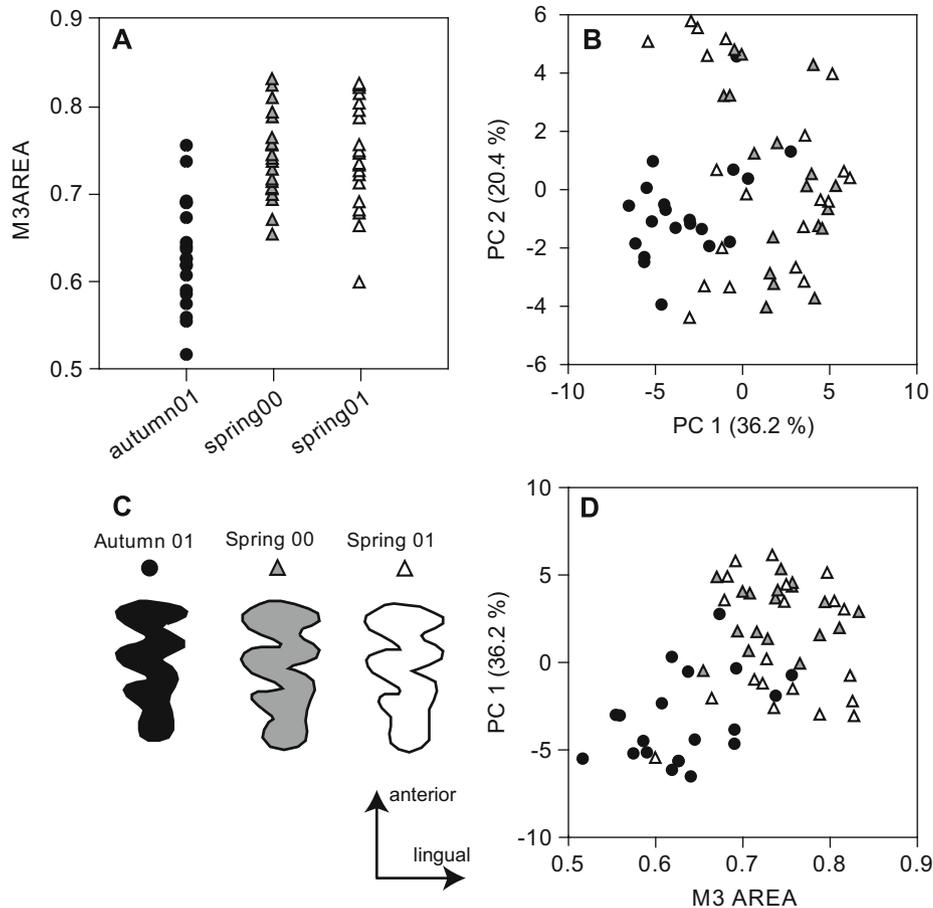


Fig. 2. Seasonal differences in the size and shape of the occlusal surface of third upper molars. (A) Size differences of M3 occlusal surface between spring and autumn populations. The area of the 2D outline is considered as the size estimator of the occlusal surface. Each dot corresponds to a single tooth. (B) Shape difference between seasons, displayed on the first two synthetic axes obtained by a PCA on the Fourier coefficients of the molar outlines. Each dot corresponds to a single tooth. (C) Reconstructed average outlines for each season of trapping, exemplifying the shape differences of the M3 occlusal surface involved. (D) Relation between the area of the teeth and the main axis of variation determined by the first principal component of the PCA.

and in spring 2001 have M3 occlusal surface of similar size (spring 2000 vs. spring 2001: $P = 0.912$), covering the same range of variation, in contrast to animals trapped in autumn 2001 (Fig. 2A) when smaller M3 occlusal surfaces occur in the population (spring vs. autumn animals: $P < 0.001$). Hence, the spring groups are not a mere sub-sample of the autumn one, despite an overlap in the size distribution.

Influence of the trapping season on the shape of the M3 occlusal surface

A test of sexual dimorphism of the molar shape showed no difference between males and females in springs 2000 and 2001 (MANOVA on the Fourier coefficients, Wilks' lambda $P = 0.100$). Males and females of each season were thus considered together.

A significant difference exists between the three groups of Pallasjärvi (MANOVA on the Fourier coefficients, Wilks' Lambda $P = 0.008$), showing that the M3 shape depends on the trapping season. The two spring samples display similar M3 shape ($P = 0.597$), differing from the autumn sample ($P = 0.003$). Accordingly, in the first principal plane of the PCA on the Fourier coefficients (PC1, 36.2% of the total variance, and PC2, 20.4%) the two spring populations overlap whereas they segregate from the autumn group (Fig. 2B). The average reconstructed outlines (Fig. 2C) show that the M3 occlusal surface in spring populations (composed of old, overwintered animals) has larger triangles in its foremost part, the posterior lobe being apparently shortened because of a backwards shift of the lingual posterior triangle. The labial posterior zone in contrast appears as straighter and longer, providing an elongated impression. In contrast the average outline corresponding to the autumn group (dominated by

young animals born in the summer) has compact, acute triangles in the foremost part of the tooth, but a short, undulated back-part.

Finally, an overall relationship seems to exist between the size and the shape of the M3 occlusal surface (Fig. 2D). Both spring samples cluster together towards large size and high PC1 scores without displaying a clear size/shape trend. In contrast the autumn group displays a wider size and shape distribution and hence, a size/shape relationship seems to emerge within this sample. The few autumn specimens with the largest occlusal surface cluster within the range of the spring samples, pointing to a common size/shape relationship in all the three Pallasjärvi samples (Fig. 2D).

3D imaging

The 3D image of a relatively unworn upper molar row (Fig. 3A) clearly shows that the posterior border of the tooth is not straight but tilted. Hence, progressive wear will affect the 2D outline of the occlusal surface by moving along this curved surface. This is exemplified by three successive slides mimicking progressive wear down the crown (Fig. 3B). The occlusal plane indeed shows a shortened and roundish back-part of the M3 typical of the autumn outline. By going down from 120 and then 320 μm , the back-part of the M3 extends and becomes more elongated in its labial posterior part,

corresponding to the reconstructed average outlines and to the observed increasing size of the occlusal surface of the spring populations.

Phylogeographic versus seasonal variability in M3 occlusal surface size and shape

The difference due to seasonal variation in the area of M3 occlusal surface is of the same order of magnitude as differences observed between distant localities in the Western lineage or between lineages such as Ural and Eastern lineages (Fig. 4A). Only the Italian and Spanish groups display a size clearly outside the range of variation covered by the seasonal variations at Pallasjärvi.

Regarding the shape of the M3 occlusal surface, the first principal plane of the PCA including all localities and the seasonal groups at Pallasjärvi expresses a large within-lineage variation without clear biogeographic structure (Fig. 4B). Except for the Spanish lineage shifted towards negative PC1 values (PC1: 29% of the total variance), the range of the different lineages overlap, leading to a weak inter-lineage differentiation on this axis (ANOVA among lineages on PC1: $P = 0.036$; without the Spanish lineage $P = 0.781$). Along the same PC1 axis, the seasonal groups at Pallasjärvi are dramatically opposed, with spring samples plotting towards positive values whereas autumn

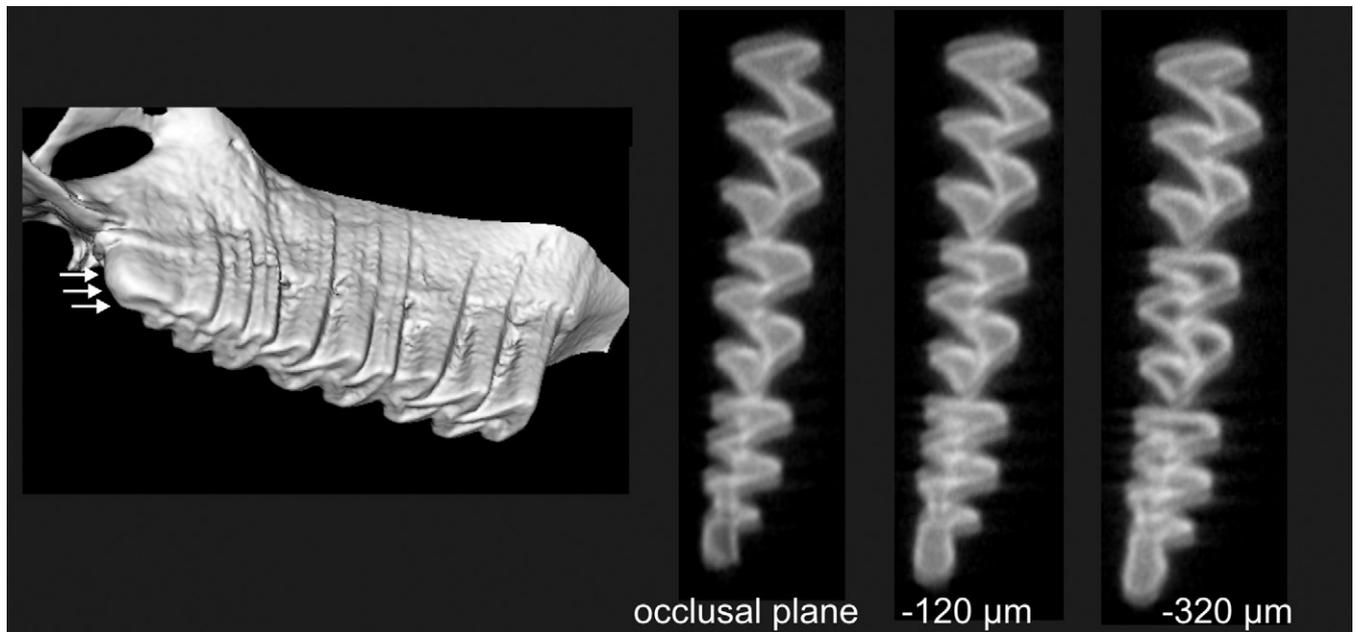


Fig. 3. 3D Image of an upper molar row and slices down the occlusal surfaces mimicking progressive wear. Left, a specimen from the autumn population 2001 with a high crown was selected for a μCT -scan, with slices spaced from 20 μm and a final pixel size of 45 μm (tomography performed by Voxcan, Lyon, France). Right, based on the 3D reconstruction, successive slices of the upper molar row were performed parallel to the occlusal surface, providing a visual approximation of the effect of progressive wear on the 2D shape of the occlusal surface.

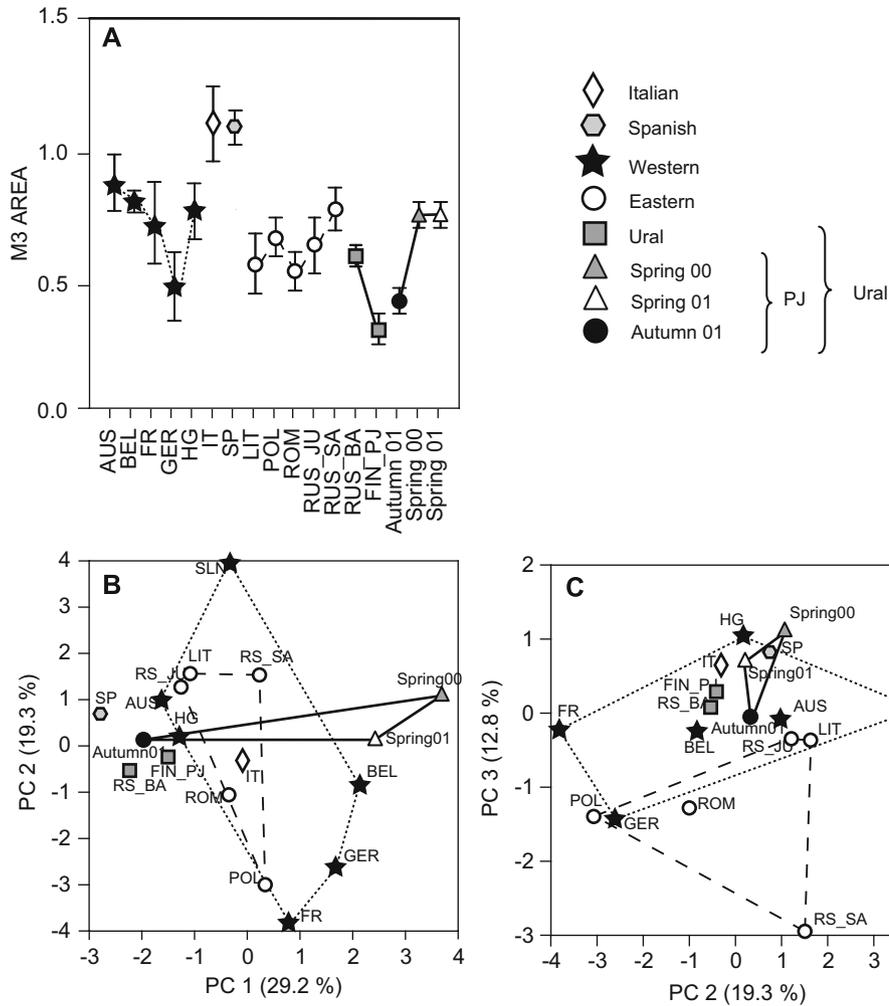


Fig. 4. Seasonal and phylogeographic variations of the shape and size of the M3 occlusal surface. Seasonal replicates at Pallasjärvi were considered together with localities sampling the geographic variation across northern Europe. (A) Size of the M3 occlusal surface, estimated by area of its 2D outline. Mean value and confidence interval of the molar area are represented for the different localities and the three seasonal replicates at Pallasjärvi. (B) and (C) Shape variation of the M3 occlusal surface, represented on synthetic shape axes obtained by a PCA on the Fourier coefficients. Each dot represents an average value per sample; symbols correspond to the lineage or season of trapping for Pallasjärvi samples. (B) First principal plane, PC1 vs. PC2. (C) Second principal plane, PC2 vs. PC3.

samples plots towards negative scores. This suggests that this axis is heavily influenced by temporal variability occurring within a given area, corresponding at Pallasjärvi to a difference between spring and autumn populations.

No phylogeographic structure emerge on the subsequent second axis (PC2, 19% of variance; ANOVA among lineages: $P = 0.773$) but geographic differences are displayed on the third axis (PC3, 13% of variance; ANOVA among lineages: $P < 0.001$). This corresponds mainly to a segregation of the Eastern lineage vs. all other groups along this axis (Fig. 4C). Noteworthy, the different seasonal samples of Pallasjärvi cluster together, and are close to the other Ural samples along this axis. Thus, inter-lineage differences emerge on this morpho-

space, by discarding the large intra-group variability characteristic of the first principal axis.

Discussion

Our study demonstrated that the size and shape of the molar occlusal surface, here the third upper molar, varies significantly in a given population of bank voles depending on the trapping season. Such an effect is not negligible compared with biogeographic differences and may thus interfere with the attempt of tracing short-term evolutionary processes based on such phenotypic characters.

Several, non-mutually exclusive hypotheses may contribute to explain such seasonal variations in the estimate of size and shape of the M3 occlusal surface. First, this may be a mere consequence of differences in age structure documented in a population at different times of the year, leading to measures of the occlusal surface on teeth worn at a different degree. The difference observed between spring and autumn samples at the same location would correspond to a difference between worn teeth observed in spring samples, composed of old, overwintered animals, and less worn teeth in autumn samples, when young animals born during summer dominate. Several evidences support this hypothesis. In the size/shape morphospace (Fig. 2C), a gradient seems to lead from small, variable autumn M3 samples to larger, less variable spring samples. This may correspond to mixed autumn populations composed of rather young animals with unworn teeth, and some older animals that overlap with the spring population exclusively composed of old, overwintered animals with worn teeth. In agreement, the tentative attempt to mimic progressive wear by successive slides down the crown on a 3D model of an unworn M3 provided significant size and shape variation of the occlusal surface that match the expected pattern based on seasonal differences. These variations would be due to a pyramidal backpart of the M3, leading to an increased occlusal surface and a change in its shape when the tooth crown is worn down.

The second hypothesis to explain seasonal differences in a population involves differential selection along the seasonal life cycle. For some reason, directly related or not to the morphology of the occlusal surface, specimens with a larger occlusal surface and larger foremost triangles on the M3 might better survive winter, whereas specimens with a reduced occlusal surface might better reproduce in summer. Only population genetics analyses may validate or discard this hypothesis (Ishibashi et al. 1997) and such a study is currently under way. Considering, however, the importance of variation in the occlusal surface only related to different degree of wear, makes the first hypothesis the most straightforward candidate to explain the seasonal differences observed.

Our results suggest that wear, and hence indirectly age, affect the outline of the occlusal surface. This variation is far from negligible compared with differentiation among lineages, being of the same order of magnitude and even emerging as the first order signal of a multivariate analysis including samples covering both seasonal and geographic variations. It may therefore interfere with tracing biogeographic history from teeth remains. Taking wear into consideration, however, may allow discarding this effect and improve the value of teeth as phylogeographic markers. Further effects may contribute to the important phenotypic variation in bank voles. We considered seasonal variations, but this

species is characterised by important multi-annual fluctuations in population density (at Pallasjärvi Henttonen 2000; Tkadlec and Stenseth 2001). These fluctuations have been attributed to various factors including predation (at Pallasjärvi Henttonen et al. 1987; Lambin et al. 2000; Hanski et al. 2001; Korpimäki et al. 2005), competition (Hansen et al. 1999), or seasonality (Tkadlec and Zejda 1998; Saitoh et al. 2003). All might influence the phenotypic characteristics of the population, directly through differential selection or indirectly through changes in the age structure and the related wear stages. Further studies are required to evaluate the importance of these sources of variation compared with geographic patterns.

Acknowledgements

We thank Vincent Laudet for his support and Jean-Pierre Quéré for stimulating discussions, as well as A.V. Borodin and an anonymous reviewer for their helpful comments. This study has been supported by the ANR “Quenottes” and GDR 2474 “Morphométrie et Evolution des Formes”.

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