



Molar shape differentiation during range expansions of the collared lemming (*Dicrostonyx torquatus*) related to past climate changes

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ABSTRACT

The genus *Dicrostonyx* (the collared lemming) is undoubtedly the small mammal best adapted to the extreme conditions of the arctic environment. The Palearctic collared lemming has been described in numerous European Late Pleistocene localities up to south of France and Croatia. This species experienced climate-driven changes through time, changes mainly observed as repetitive pulses of pan-continental migration, and it thus became a typical indicator of glacial conditions. Using geometric morphometrics on molars, we evaluate the shape changes occurring during the last 100 ky over some dispersal events in Western Europe. The results point out that *Dicrostonyx torquatus* has a large intra-population variation with a homogenous morphology, regardless of the origin of the individuals. A temporal trend leading to a more complex tooth with a differentiated anterior loop on the first lower molar was observed. An additional effect of the distance from the core populations was also described with a more peculiar shape for the most western populations of France. These temporal and geographical trends might relate to the different migratory pulses documented from ancient DNA haplotypes.

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1. Introduction

The Arctic is unique among Earth's ecosystems and covers almost ten percent of land area. Restrained to circumpolar locations, north to the timberline, this region is subject to extreme climate conditions associated with strong seasonality. Despite the restrictive environment for plant development and limited available resources, many animals inhabit this region such as among terrestrial mammals, some carnivores (*Ursus maritimus*, *Canis lupus arctos*, *Vulpes lagopus*), some large herbivores (*Alces alces*, *Rangifer*

tarandus), some lagomorphs (*Lepus arcticus*) and several small mammals (*Sorex arcticus*, lemmings and voles). These species exhibit different strategies, as migration or hibernation, to cope with the hard conditions and survive (Blix, 2016). In this ecosystem, rodents constitute the main resources for numerous predators and the cyclic dynamics of these key-species is a major driver of the fluctuations of the tundra food web (e.g., Gilg et al., 2003). The collared lemming (*Dicrostonyx*) represents an emblematic species-complex of this peculiar landscape. This small mammal is well adapted to these conditions, living in dry and well-drained uplands in high Arctic tundra and forest tundra (Wilson et al., 2017).

The different species of *Dicrostonyx* have a range covering a nearly circumpolar area from Alaska, Canada, Greenland up to Western Russia and North-East Siberia (Wilson et al., 2017). The Eurasian species, *Dicrostonyx torquatus* (the Palearctic collared

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lemming) is divided into five phylogenetic clades (Fedorov et al., 1999; Fregda et al., 1999; Abramson and Tikhonova, 2002), congruent with the geographical distribution of chromosome races (Fedorov et al., 1999). This genetic structure seems to derive from the fragmentation of the species' range in the Late Pleistocene and to bottleneck events during the Holocene thermal maximum. The Late Pleistocene is characterized by many major shifts in climate, with both stadial and interstadial cycles known as abrupt and short Heinrich or Dansgaard-Oeschger events (e.g. Labeyrie et al., 2007). These climate fluctuations led to important contraction, expansion or shift in many species' ranges (Hewitt, 1996, 2000), generating migrations and/or local extinctions. These responses appear mainly individualistic (Stewart, 2009) and thus led to changes in species associations and richness establishing non-analogue communities compared to extant ones (e.g., for small mammal assemblages see Kowalski, 1995; Royer et al., 2016). These transient communities contain novel biotic interactions (Blois et al., 2013) since each species has its own capability to track rapid climate change, capacity that appears at least partly related to its own traits (Angert et al., 2011; MacLean and Beissinger, 2017). The collared lemming experienced these climate-driven changes through time, becoming a typical indicator of glacial conditions in the past literature (e.g., Chaline, 1972; Harlé, 1906; Hinton, 1926; Kowalski, 1995). Indeed, this species was recognized between the middle of 19th and the beginning of the 20th centuries in many different fossil records located far South of its current Arctic range, as in Germany (Hensel, 1855), England (Sanford, 1870), Belgium (Rutot, 1910), France (Harlé, 1893, 1906; Pomel, 1853), or Croatia (Lenardić, 2013). Although, many sub-specific or specific taxa of fossil collared lemmings were described from the Late Pleistocene in Europe (e.g., Friant, 1960; Hinton, 1910, 1926; Sanford, 1870), whose relevance remains highly questionable according to Kowalski (2001), the occurrences of these taxa at least attest repeated colonisations of Western Europe throughout different climatic cycles. Based on ancient DNA, populations appear to have been regularly affected by Dansgaard-Oeschger interstadial events all along their presence in Western Europe (Brace et al., 2012), corroborating assumptions from fossil remains (e.g., Marquet, 1993; Royer et al., 2016; Villa et al., 2010). One expected outcome of these repetitive range shifts and/or expansion with local extinctions and subsequent recolonizations is a reduced genetic divergence among populations (Martin and McKay, 2004). These events are also expected to reduce the within-population genetic diversity in peripheral populations (Eckert et al., 2008) by a series of successive bottlenecks (Hewitt, 1996) and genetic drift enhancing the surfing of peculiar alleles over large geographical areas (Klopstein et al., 2005) but with sharp differences between areas (Excoffier and Ray, 2008). Increase of mutation load in populations on the expansion front is also expected from the same phenomenon (Peischl et al., 2013; Willi et al., 2018), which led to strong divergences of peripheral populations. Following the Last Glacial Maximum, population declines of the collared lemming have been evidenced and climate changes occurring at that time have thus strongly impacted them, affecting their effective population sizes and their genetic diversity (Prost et al., 2010). The last occurrences of the collared lemming in Western Europe vary from the Bølling-Allerød to the early Holocene according to the latitude (e.g., Cordy, 1991; Kowalski, 1995; Price, 2003; Royer, 2013; Royer et al., 2016).

In this context of past climate changes and major range expansions and contractions, the aim of this study is to evaluate the shape variation of the collared lemming teeth, through time and space, from fossil and extant specimens. Indeed, even if there are some studies describing the morphology through biometrical and morphotype analyses (Abramson et al., 2004; Agadjanian, 1976;

Agadjanian and Koenigswald, 1977; Kochev, 1984; Nadachowski, 1982; Nagel, 1997; Ponomarev and Puzachenko, 2015; Smirnov et al., 1986, 1997; Zazhigin, 1976), very few studies have investigated morphological variation of this species at large temporal and spatial scales. In the Palearctic collared lemmings, skull and mandible morphologies vary in agreement to chromosome races and mtDNA clades, relationship congruent with the Late Pleistocene stadial cycles (Abramson and Tikhonova, 2002).

In the current study, we investigate the shape of molar as this anatomical element presents two main advantages. First, it allows the comparison of modern and fossil individuals, as it represents the best-preserved fossil remain that can usually be identified at the species level. Second, teeth harbour less plasticity compared to skull and mandible, and thus are likely to vehicle more information to be compared with haplotype diversities. In lemmings, the upper teeth have mainly been studied for systematics purpose in order to discriminate species or simplex and complex morphotypes. We focused instead on the first lower molar because this dental element is also well studied in voles and lemmings for a very long time in evolutionary studies. Moreover, this molar has the special attractiveness of being recently examined in developmental studies (e.g. Harjunmaa et al., 2012; Peterková et al., 2006; Salazar-Ciudad and Jernvall, 2002; Renvoisé et al., 2018). These interests allow potential comparisons aimed at a better understanding of evolutionary patterns and processes in this rodent group (Kavanagh et al., 2007; Polly, 2007; Renvoisé et al., 2009). Geometric morphometrics of the tooth shape was investigated through a temporal sequence ranging from MIS 6 to MIS 1 and a geographical gradient from Siberia to southwestern France. This unique dataset provides the opportunity to contrast morphological variation with the known genetic differentiation observed in recent paleogenetic studies (Palkopoulou et al., 2016), in order to understand the evolution of the Palearctic collared lemming during its Late Pleistocene geographical expansion in Europe.

2. Material and methods

A total of 592 first lower molars were sampled from 16 fossil localities and 2 present-day sites (Fig. 1; Table 1). All specimens came from collections of Natural History Museums or research laboratories. The fossil sites are located throughout in Europe, mainly in France, Belgium, Switzerland, Hungary and Poland (Fig. 1). They extended from MIS 6 for the oldest site located in Poland up to the Bølling period (see description of sites in supplementary materials). Fossil populations have been gathered in order to obtain a representative temporal succession both of the haplotypes characterized with ancient DNA and major climatic changes for the studied period (Fig. 2). The present-day specimens were collected between 2013 and 2015 at two field stations located in the Yamal Peninsula, Siberia: Erkuta and Sabetta (Fig. 1). Following several authors (Abramson and Tikhonova, 2002; Fedorov et al., 1999; Fregda et al., 1999), these modern lemmings belong to the karyotype I and haplotype B, i.e. *Dicrostonyx torquatus* (Wilson et al., 2017).

Dicrostonyx is a genus with a large morphological variability. The molars are rootless and without cement in the re-entrant triangles. The first lower molar is composed of a posterior loop, usually seven closed triangles plus one or two supplementary triangles opened in the anterior loop leading to more or less complex teeth (from seven, to eight and even nine triangles). The presence of *Dicrostonyx* genus is also well recognized in the fossil material with the upper second molars that possess four closed triangles and an external posterior lobe.

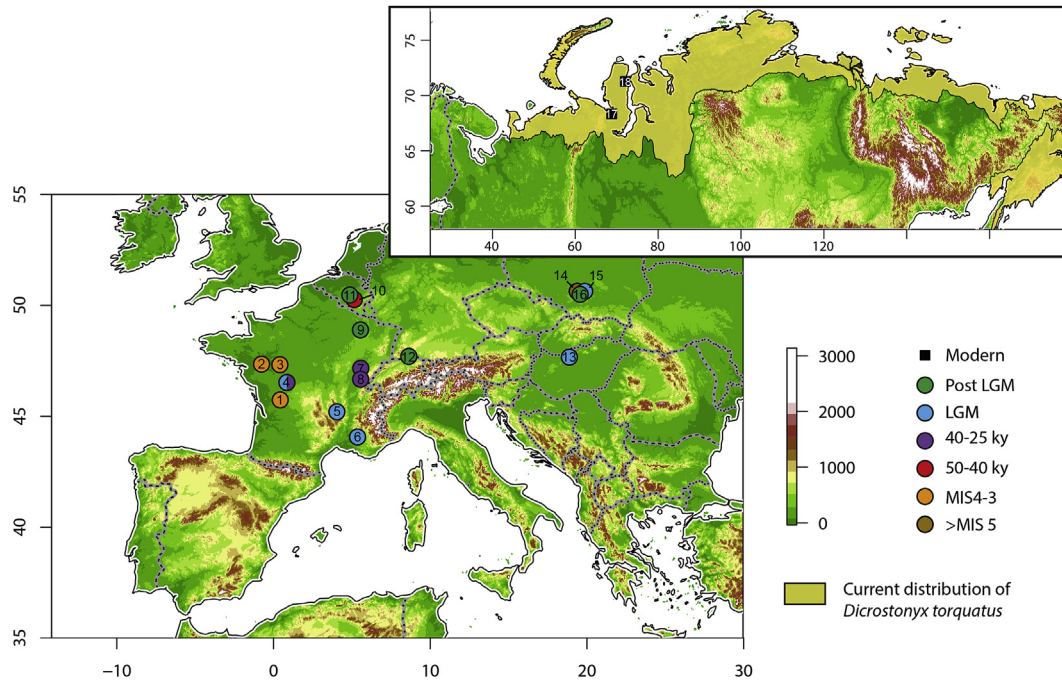


Fig. 1. Map of fossil and extant localities with *Dicrostonyx* sp. Colours are according to the age category from the oldest locality (>MIS5) to the youngest sites (Post-LGM). The two modern sites (black squares) are located in Siberia (Yamal Peninsula). The localities are numbered according Fig. 2. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 1

List of modern and fossil sites reported with the number of analysed teeth.

	Localities	Region	Age category	Number of teeth
Modern samples	Erkuta	Yamal (Siberia)	Modern	12
	Sabetta	Yamal (Siberia)	Modern	11
Fossil samples	Tailles des Coteaux Young	SW France	LGM	17
	Tailles des Coteaux Old	SW France	40-25 ky	21
	Les Pradelles	SW France	MIS 4-3	83
	La Roche Cotard	SW France	MIS 4-3	23
	Roc en Pail	SW France	MIS 4-3	41
	Cottier	SE France	LGM	9
	Coulet des Roches	SE France	LGM	21
	Roche Plate	NE France	Post-LGM	78
	Amange	NE France	40-25 ky	23
	Baume de Gigny	NE France	40-25 ky	7
	Chaleux	Belgium	Post-LGM	42
	Marie Jeanne	Belgium	50-40 ky	83
	Schweitzersbild	Switzerland	Post-LGM	20
	Pilisszanto	Hungary	LGM	10
	Deszczowa Cave	Poland	>MIS 5	31
Mamutowa Cave	Poland	LGM	29	
Oblazowa Cave	Poland	Post-LGM	31	

2.1. Landmark acquisition

Landmarks and semi-landmarks were acquired following the protocol described in Navarro et al. (2018). All teeth were first drawn under a binocular coupled with a camera lucida at a 25× magnification. Tooth orientation was standardized by setting its elongation axis as vertical and by optimizing the focus along its occlusal plane. The drawings were then scanned using a 600 dpi resolution. Following the protocol of Brunet-Lecomte (1988) and Laffont et al. (2009), landmarking process was automated by first standardizing the orientation according to the manual marking of two landmarks (L3 and L19 in Fig. 3) enabling the automatic detection of 11 additional landmarks defined as extreme tips of salient and re-entrant triangles and loop tips. Because the anterior

part of the tooth in voles is tilted towards the labial side, a second standardization was taken based on the manual marking of two additional landmarks (L8 and L18), enabling to detect automatically five landmarks on extreme tips. In total, four landmarks are manually marked and 13 additional landmarks are automatically detected. All landmarked teeth were further checked for gross error. Additionally, twenty semi-landmarks, equally distributed along the outline between the landmarks 10 and 16, were added to better characterize the anterior loop. This automatic protocol has been written in R language and is available on request from the authors.

2.2. Geometric morphometrics

A partial Generalized Procrustes Analysis (GPA) was used to

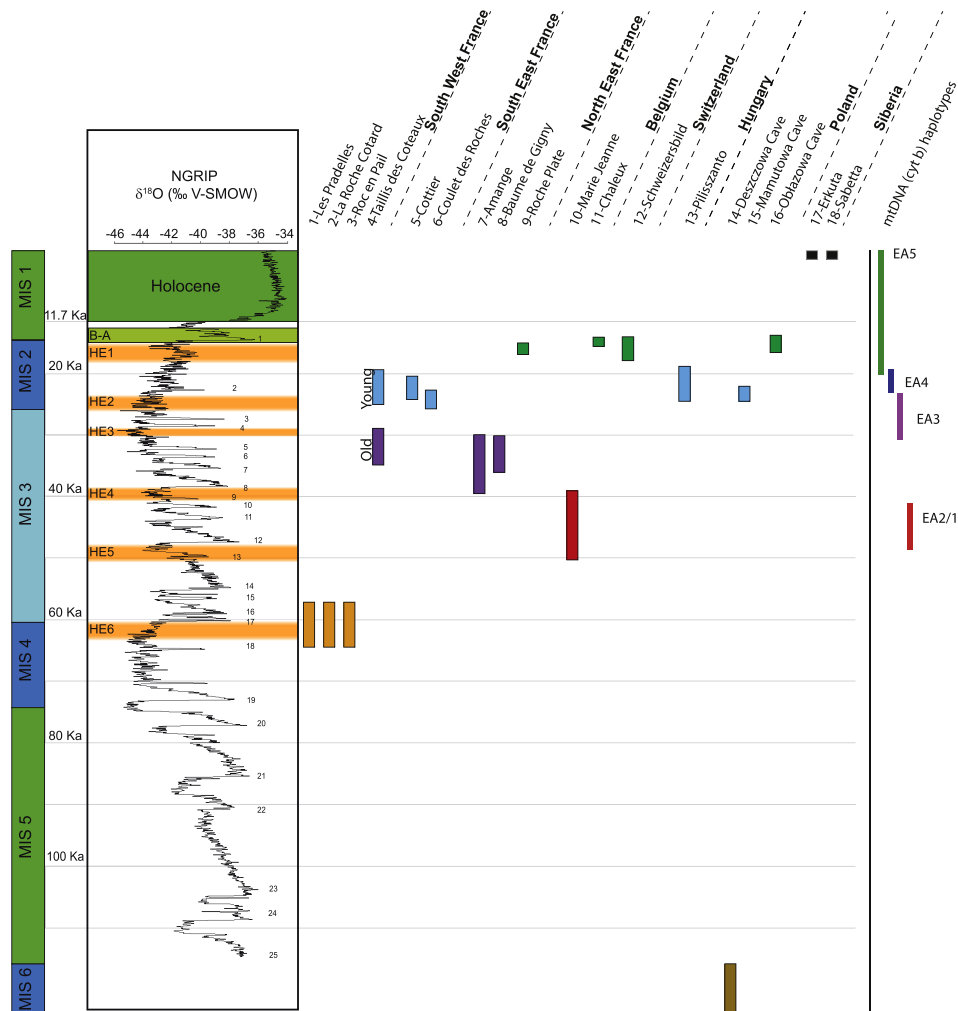


Fig. 2. Chronology and climatic context of sampling sites. Mitochondrial DNA clades from Palkopoulou et al. (2016) are reported.

remove all non-shape components (position, size and orientation) by means of rigid transformations (Dryden and Mardia, 1998), and semi-landmarks were sliding by minimizing the bending energy (Bookstein, 1997). Procrustes coordinates were then projected onto an Euclidean tangent space. Based on Mahalanobis distances, 28 outliers were removed. They were distributed across several populations. As tangent space coordinates are rank-deficient variables, we rotated the data using principal component analysis (PCA) and removed axes with null eigenvalues prior to further analyses. Additionally, a between-group PCA was performed to display patterns of differentiation among populations.

A multivariate regression of shape to ages and geographical distances was done to evaluate whether shape is structured across time (as described in Fig. 2) and space. For the latter, great circle distances were calculated between the different localities and Siberia. Both Procrustes ANOVA (Goodall's F-test) and MANOVA (Pillai's trace) were computed and their significance assessed using 1000 permutations. Effect sizes were computed as the percentage of Procrustes sum of squares explained (Monteiro, 1999) as well as the percentage of regression projection scores explained (Maga et al., 2015; Navarro and Maga, 2016). Whereas the former account for the overall effect, the latter focused on the specific direction of the shape space described by the effect. The shape changes associated to each effect were then visualized against the

mean shape according to a scaling corresponding to 3000 km and 200 ky.

Within-population variance was computed as the sum of squared Procrustes distances between individuals and the population mean shape. Standard errors were based on 200 bootstrap resampling. A modified Levene test based on Procrustes distances and 1000 permutations was performed to evaluate whether the levels of diversity were different among the populations.

GPA and Procrustes ANOVA were realized with geomorph version 3.0.6 (Adams et al., 2018), and all other analyses were performed using our own R codes and ran in R 3.5.2 (R Core Team, 2018).

3. Results

The two first principal components (PCs) of the molar shape account, respectively, for 18.2% and 14.3% of the total shape variation (Fig. 4A). The variation appears to be quite lowly structured and spreads on many dimensions on the shape space, with 23 PCs accounting for 90% of the variation. The result points out a homogenous morphology for the species, regardless of the origin of the individuals. Fig. 4B shows the mean of the different localities on PC1 and PC2 according to age categories. Despite a large overlap in morphology, PC1 shows that few recent localities (on the positive

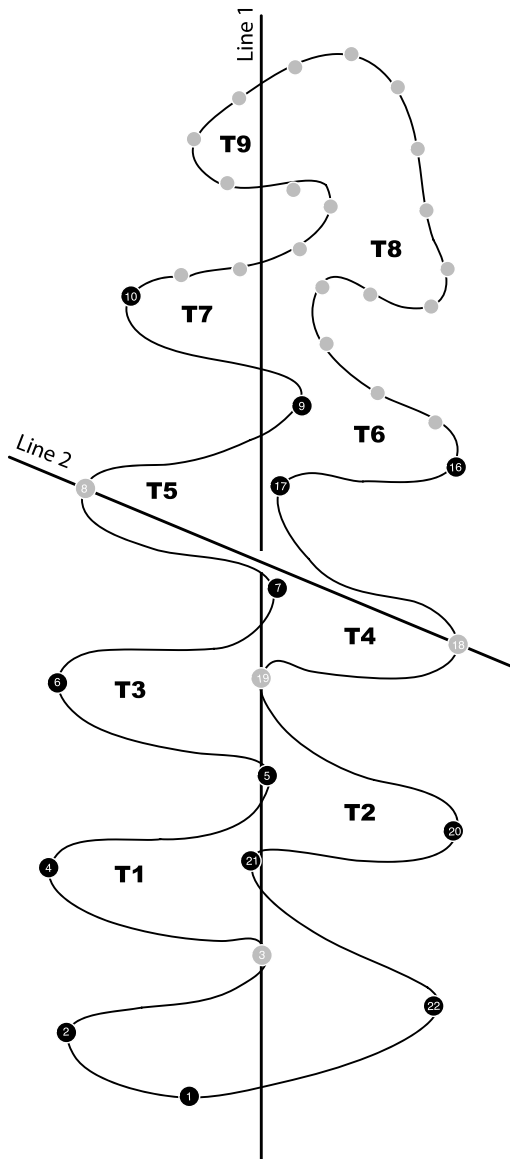


Fig. 3. Schema of landmarks (numbered dots) and semi-landmarks (small dots) used to describe the first lower molar of *Dicrostonyx* sp. The white numbered dots are operated manually and the black ones are automatically detected. Tooth nomenclature is as follow: Triangle (T), Anterior Loop (AL).

part of the axis), such as Chaleux, Schweizersbild and Sabetta, are opposed to oldest ones (on the negative part), such as Deszczowa, Amange and the recent level of Taillis des Coteaux (TDC Young). On PC2, eastern localities such as Amange, Gigny and Sabetta (on negative part of the axis) are opposed to sites located in the southwestern (TDC) or southeastern France (Coulet des Roches) on the positive part. The main variation on PC1 concerns the anterior loop of the tooth, with an increase in complexity carried by the two last triangles (T8 and T9), which are more widened. In comparison, the posterior part (triangles T1 to T5) looks like very stable. On PC2, variation relates to a tilt from the external triangles toward the internal side of the tooth.

To focus only on the variation among population, a between-group PCA was performed. The two first principal components (bgPCs) resume 56% of the among population variance. These two bgPCs highlight a robust morphological contrast between fossil and modern morphologies (Fig. 5). The two present-day populations from Siberia are individualized on the most positive parts of PC1

and PC2. Fossil populations are organized according to a composite signal combining time and geography. A temporal signal is observed from the old sites on the negative part of PC1 to the more recent sites on the positive part. When a large geographical range was sampled synchronously across Europe, as it is the case for the LGM period, a differentiation between western and eastern fossil populations could also be noticed (Fig. 5). Shape variation on PC1 is mostly expressed on the anterior loop by more pronounced triangles. This shape change seems to characterize the most recent populations. Shape changes associated to PC2 reflects a tendency to torsion, especially on the posterior loop and on T5 and T7 triangles. As PC2 opposes mainly the modern and ancient populations, these specific morphologies characterized the two modern populations of Yamal.

To evaluate the significance of the observed spatio-temporal patterns, a multivariate regression of tooth shape on age and geographical distance to Siberia was generated. Due to their geographical peculiarity compared to the rest of the samples, the two Siberian populations were dropped from the analysis. The results (not shown) when Siberian populations are included, were in line with those presented hereafter. The linear trend related to locality ages (Fig. 6A) is significant (MANOVA: $F_{72, 467} = 3.08$, $p < 0.001$; Procrustes ANOVA: $F_{1, 538} = 7.91$, $p < 0.001$). This age effect explained 1.44% of the total shape variance and 10.4% of the variance of the regression scores (Fig. 6A). As for the PCA analysis, most of the variation is carried by the anterior loop of the tooth with the same pattern of complexity through time. The two modern populations from Yamal (400 km apart), for which scores were recomputed as supplementary observations, are different with no overlap between them. The regression scores of localities from the MIS4/3 and 40–25 ky show a similar range of variation, whereas the ones from the LGM have the largest variation between localities. Interestingly, western localities (TDC young and Coulet des Roches) were also clearly separated from eastern sites (Pilisszanto and Mamutowa; Fig. 6A).

The linear trend related to the geographical distance from Siberia (Fig. 6B) was also significant (MANOVA: $F_{72, 467} = 2.51$, $p < 0.001$; Procrustes ANOVA: $F_{1, 538} = 3.86$, $p < 0.001$). This effect explained 0.7% of the total shape variance and 6.7% of the variance of the regression scores. It opposes the three localities from Poland against those from the southernmost France, such as TDC, Coulet des Roches or Les Pradelles. The sites of Hungary, Belgium and eastern France are closer to the sites of Poland than to the ones from the south of France, regardless of their ages. The morphological variation is less marked compared to the age effect but it mainly concerns again the anterior loop (Fig. 6B).

Points of caution can be raised concerning some localities. The age of Marie Jeanne (Belgium) is not yet stabilized. It falls into the limit of radiocarbon methods and may therefore be older than 50 ky (López-García et al., 2017). If so, Marie Jeanne can be compared to the three sites from the southwest France dated from MIS4–3. The ages of Les Pradelles and La Roche Cotard vary between the Heinrich 6 event and 50 ky (Frouin et al., 2017; Marquet et al., 2016). Despite these age uncertainties, the same results with a morphological differentiation between the two western sites (Les Pradelles and Roc-en-Pail) from those of the eastern sites and the one from Belgium are observed.

Within-population Procrustes variances were different among fossil populations (Levene test: $W_{16, 524} = 1.98$, $p = 0.013$). Similar result (Levene test: $W_{11, 474} = 2.38$, $p = 0.008$) was observed without the four populations with a sample size lower than 19 (Cottier, Gigny, Pilisszanto, TdCYoung). The Procrustes variance seems to steadily increase according to the distance from the source until to drop in the most western and southeastern populations

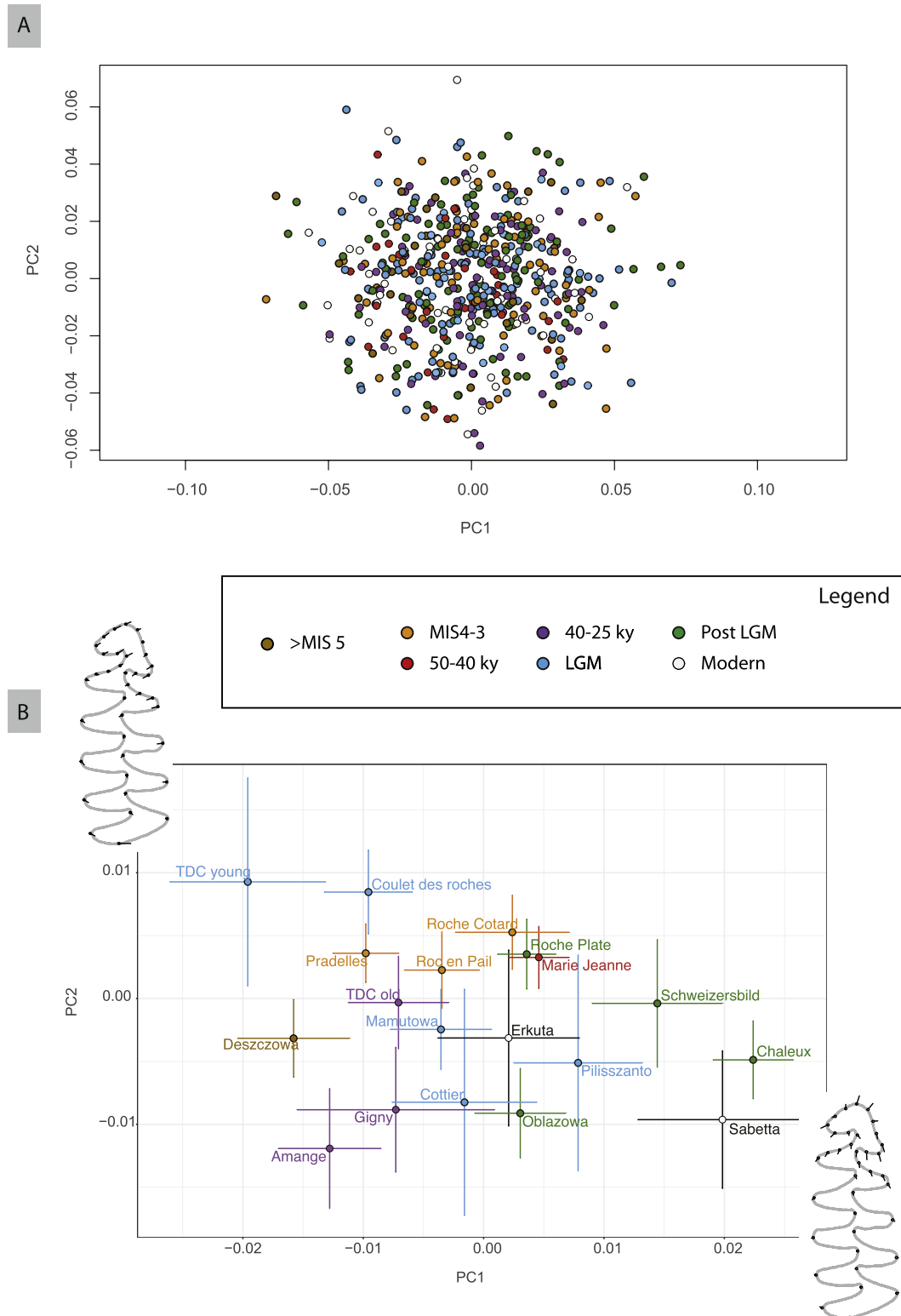


Fig. 4. A. Morphospace (as PC1-PC2 plane) of all fossil and modern specimens. B. Morphospace (as PC1-PC2 plane) of the mean of each locality. Coloured dots are according to the age categories. Shape changes from the mean shape associated to PC1 and to PC2 have been drawn.

(Fig. 7). This trend was marginally significant once the three low variance populations were removed ($\rho = 0.51$, $p = 0.06$). Both more individuals for some localities and more sites are necessary before to reach robust conclusion.

4. Discussion

The geometric morphometrics analysis of the first lower molar based on samples distributed largely across time and space shows

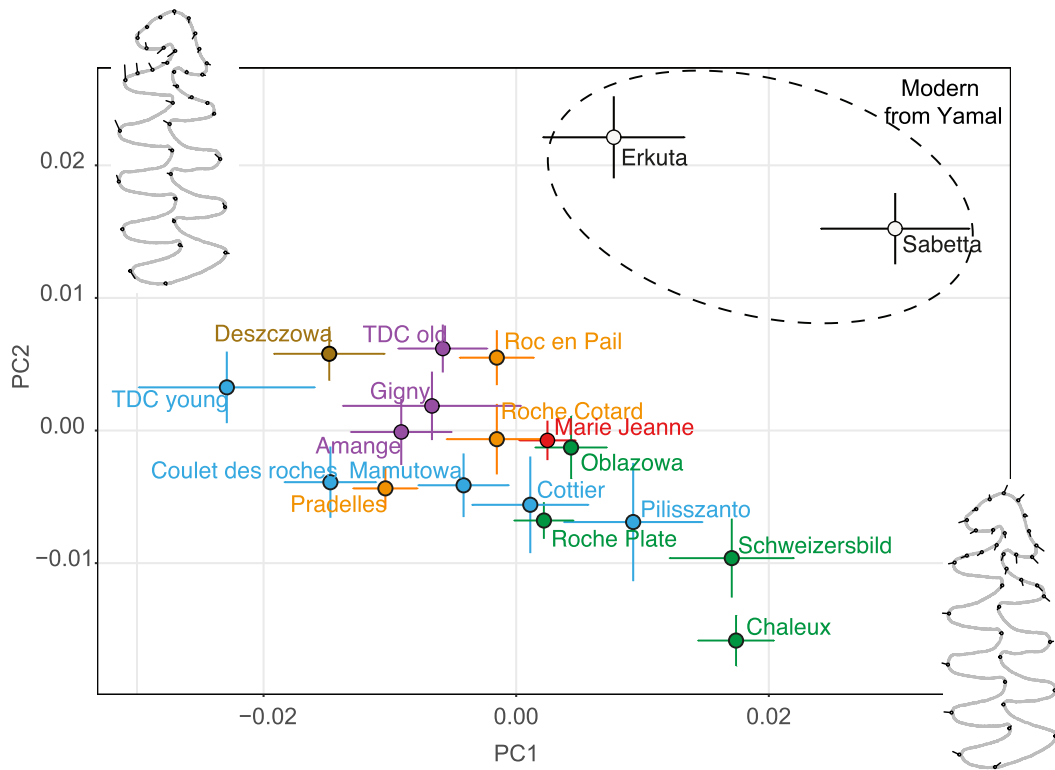


Fig. 5. Morphospace (as PC1-PC2 plane) based on the between group principal component analysis (BGPCA) with the mean of fossil and modern localities. Shape changes from the mean shape associated to PC1 and to PC2 have been drawn. Colours represent the age categories. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

that both modern and fossil specimens exhibit a quite variable morphology, but this variation is almost similar among populations. Indeed, this variation is spread on many, if not all, directions of the morphospace and a large intra-population variance has been observed both temporally and geographically. This pattern is frequently observed at the intraspecific level on tooth shape (e.g., Navarro et al., 2018; Renaud and Michaux, 2007; Renvoisé et al., 2011). This high-unexplained variation could result from wear (Ledevin et al., 2010), from the interactions of many factors with relatively small main effects (Caumul and Polly, 2005) or from stochasticity during tooth development (Salazar-Ciudad and Jernvall, 2010).

The between-group PCA analysis, by focusing only on the inter-population variance, could efficiently track differences among populations and thus showed a strong pattern of differentiation between fossil and modern localities. The main shape change between these two temporal sets is observed on the anterior loop with modern specimens exhibiting a more derived and complex pattern with a more developed anterior loop (well-drawn T8 and T9 triangles). Developmental studies have suggested that this increase in complexity (i.e., addition of a new cusp) seems to be slower than a decrease in complexity because it requires multiple changes in developmental regulation (Harjunmaa et al., 2012). Given such low rate and the time scale covered by our samples, a complete change from a simple shape towards a complex one with well-delineated successive steps could not be observed. Difficulties lie in the characterization and the designation of all the intermediate stages (Salazar-Ciudad and Jernvall, 2010) as the acquisition of a new cusp, in the case of voles and lemmings, appears to be continuous through time (Kowalski, 1977; Nadachowski, 1992; Smirnov et al., 1986). It means that the addition is progressive and that we can usually first detect the occurrence of a bud before a new triangle is

complete.

A similar pattern has been described on the first and second upper molars of the collared lemming with an increase in complexity by progressive addition of new elements in the posterior part of the teeth (e.g., Agadjanian and Koenigswald, 1977; Ponomarev and Puzachenko, 2015; Smirnov et al., 1997). These observations have led to the description of various forms used either as morphotypes, chronospecies or species according to authors (Kochev, 1984, 1993; Ponomarev and Puzachenko, 2015; Smirnov, 2002; Smirnov et al., 1997). The modern lineage of *D. torquatus* seems to appear at the end of Late Pleistocene/beginning of Holocene (e.g., Horáček and Sánchez Marco, 1984; Nadachowski, 1982; Ponomarev and Puzachenko, 2015; Smirnov et al., 1986). From the middle Pleistocene, two temporal species have been described (Fejfar, 1966; Kowalski, 1977), but appeared as two extreme morphotypes of *D. torquatus* based on both upper and lower molars (e.g., Chaline, 1972; Jánossy, 1954; Kowalski, 1977; Sutcliffe and Kowalski, 1976). Similarly, populations of the Late Pleistocene mainly differ by the percentage of several morphotypes (Jánossy, 1954; Kowalski, 1977, 1995) and their taxonomic value is hence questionable (Kowalski, 2001; Ponomarev and Puzachenko, 2015). Our result supports this view that the differences between asynchronous fossil populations are mainly in the proportion of these different states rather than in differences between homogeneous populations and that European Late Pleistocene *Dicrostonyx* are thus ascribed to *D. torquatus*.

Despite the high within-population variation relative to the inter-population differentiation conveying the impression of a relative homogeneity through time and space, a temporal trend was observed. However no typical age-related morphology could be defined as a morphotype. This trend seems to be more a question of changes in the main proportions of the diverse

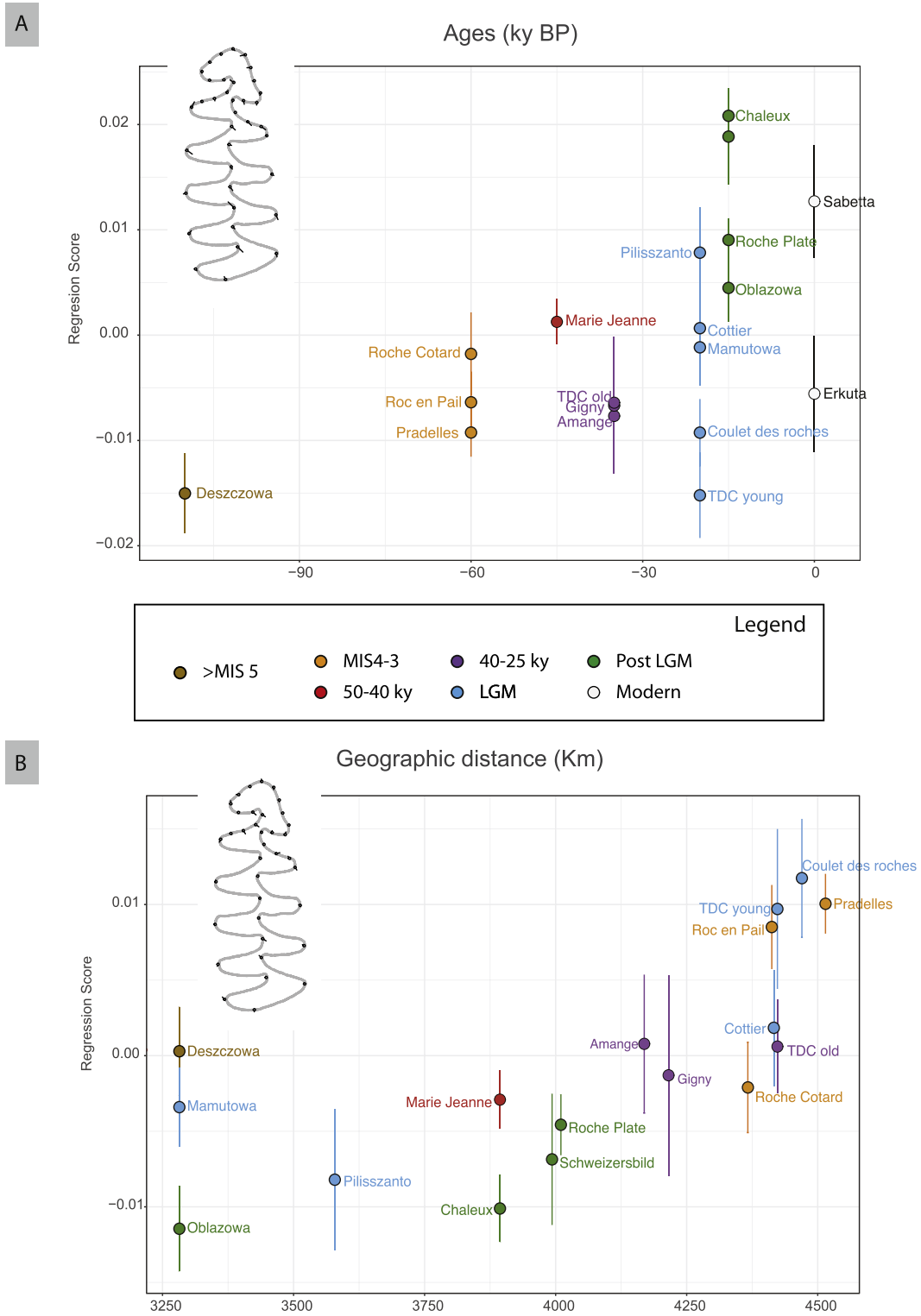


Fig. 6. A. Multivariate regression of shape to ages with the fossil localities gathered by age group and B. Multivariate regression of shape to geographical distances (B). Great circle distances were calculated between the different fossil localities from Siberia. The shape changes associated to each effect are shown against the mean shape according to a scaling corresponding to 3000 km and 200 ky.

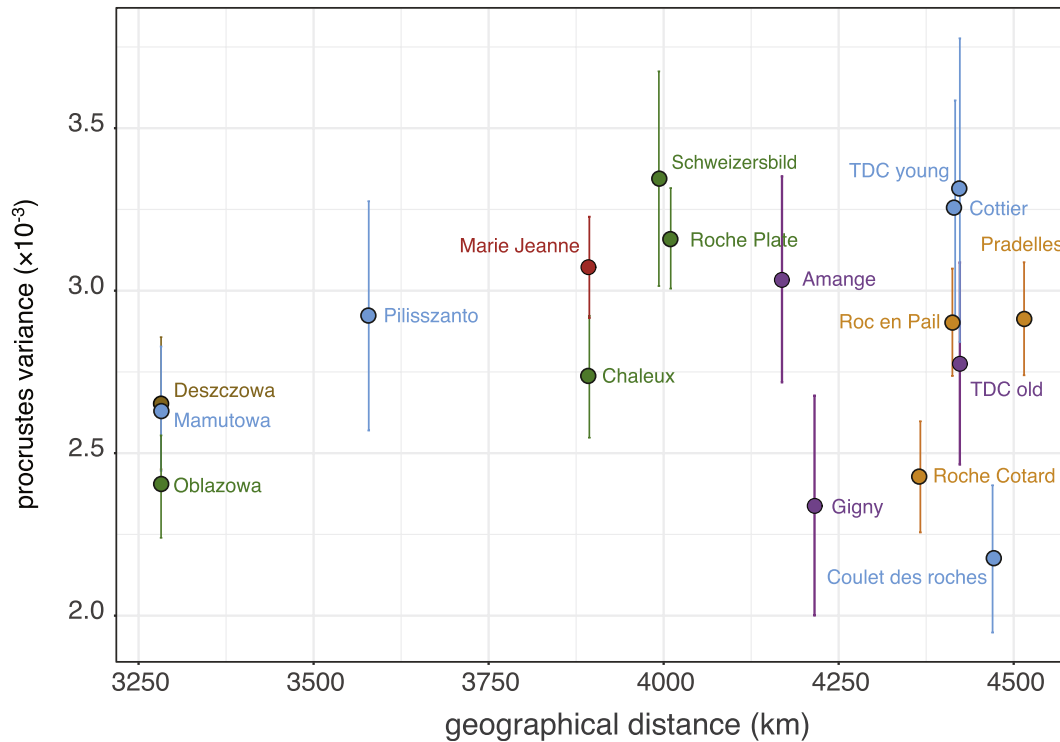


Fig. 7. Within-population variance computed as the sum of squared Procrustes distances between individuals and the population mean shape. Standard errors were based on 200 bootstrap resampling. Colours are according to Fig. 1 and represent the age category. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

morphologies than in successive turnovers of new forms. It confirms that the setting of new cusp is a relatively progressive process with a rather large variance, requiring longer time sequence to record a complete turnover. This contemporaneous large variance, without much spatial component, questioned the adaptive value of new cusp and the complexity increase of the anterior part of the tooth. In voles and lemmings, it is thought that additional cusps by increasing enamel perimeter of the tooth provide better resistance properties to abrasion and probable selective advantages in arid conditions (Barnosky and Bell, 2003). Whereas it has been shown that the prismatic and hypselodont vole and lemming teeth have clearly a selective advantage at the onset of Quaternary cycles (Renvoisé et al., 2009), a direct relationship between the increase in complexity and an adaptive value remains difficult to demonstrate at the species level (Renvoisé et al., 2011). Indeed, phylogeographical history could have a greater effect on tooth variation than climate in some vole species (Renvoisé et al., 2011).

Recently, paleogenetic studies identified five mitochondrial lineages of *D. torquatus* that succeeded each other across Europe and through time indicating a history of repeated local extinction and dispersal phases (Brace et al., 2012; Palkopoulou et al., 2016). These events are likely indicative of large-scale changes in climate and environments between steppe and tundra in Western Eurasia during the last glaciation (Palkopoulou et al., 2016). Collared lemming populations were thus able to colonize large territories by successive pulses as soon as the climate was favourable. These migratory pulses operated on a short time scale as several successive haplotypes were described on a relative short time lap (Palkopoulou et al., 2016). In the absence of local adaptation, population persistences and equilibrium between gene flow and drift, a pattern of isolation-by-distance could have arisen within an event (Hutchinson and Templeton, 1999; Orsini et al., 2013). The repetitive pulses would have structured the differentiation according to

each time period because of the uniqueness of each event: expansion settles in a core population that has evolved between pulses (Excoffier et al., 2009), and the contingencies along the migration pathways have also unpredictable outcomes related to genetic drift in small populations at the expansion front (Hallatschek and Nelson, 2008; Slatkin and Excoffier, 2012).

The temporal trend observed in molar shape could partially be related to the turnover of haplotypes identified with ancient DNA, which are relatively well circumscribed in time. While significant, this trend explains only a little part of the total shape variation. However, all shape variants exist at any period of time meaning that there was no strict correspondence between shape and haplotypes for a given period. Nonetheless, when we look at the morphology at a given geographical place, but at distinct time periods (e.g. Taillis des Coteaux Old versus Young, or Marie-Jeanne versus Chaleux), a clear differentiation can be observed. We could also note that when the effect of time was evaluated according to age categories rather than with a linear trend, then the explained total variance increases to 5% demonstrating some commonness of synchronous populations across Europe beyond the long-term trend. These results are in agreement with the hypothesis of a turnover of local populations from a new dispersal event (Fedorov, 1999; Fedorov and Goropashnaya, 1999; Fedorov et al., 1999). The populations might have dispersed at the favour of a cold event but did not adapted locally and settled on the long term. Instead, populations likely got locally extinct between favourable events. According to this assumption, pulses of migration followed rapid climate fluctuations and led to successive (but discontinuous) renewals of local populations, even if the local fossil records suggest semi-continuous occupation of the locality. Through these pulses, populations of collared lemming reach up to the southernmost region of France. They are the most extreme meridional records of lemming occurrences in Western Europe, regardless the Late

Pleistocene periods. Fossil occurrences from the southwestern France have suggested such discontinuous presence of this rodent in this region, whose high abundance correlates with Heinrich events, in particular the 2 and 3 (Royer et al., 2016). The arid and cold climatic conditions of these harsher events should have facilitated dispersal of *Dicrostonyx* sp. throughout Europe. It may also explain its presence in older sites as in Les Pradelles, which could be correlated with Heinrich event 6 (Royer et al., 2013; Frouin et al., 2017). The abruptness of these events could explain the fast dispersal of the lemming, whereas the shortness of this phenomenon associated with high fluctuations prevented the persistence of isolates.

Beyond time, our results show a geographical differentiation in agreement with the distance from the supposed pool of source populations located in the Eastern Palearctic. Indeed, it has been shown that ancient DNA haplotypes are regularly renewed by migration (Palkopoulou et al., 2016). Eastern populations were likely more stable during longer period than western and especially southern populations, emphasizing their status of source populations. Migration pulses at the favour of cold events allow lemmings to reach the south of France through Eastern and Central Europe and to diverge from the core region by genetic drift and other demographic processes along the way of the expansion such as accumulation of bottlenecks and founding events (Hewitt, 1996) or surfing effect (Klopstein et al., 2005; Excoffier and Ray, 2008). The shape differentiation between eastern and western localities can be related to such processes of divergence during range expansion. Demographic effects at the expansion front are thought to reduce genetic diversity (Hewitt, 2000), to fix peculiar variants (Excoffier and Ray, 2008) and to even accumulate deleterious alleles (Peischl et al., 2013; Willi et al., 2018). These processes might underlie the peculiar morphologies and the lower variance of some southernmost samples, which are transient populations at the expansion front. The suggestive geographical trend in variance with Northwest and East populations showing higher variance than far eastern populations needs more investigation before to reach robust conclusions and validate our hypotheses. Such pattern could result from the admixture of different source populations in these peripheral but better connected populations than the more distant southernmost populations.

The population of Chaleux (Belgium) also shows a peculiar morphology. Question about its chronological attribution still remains open, since it can be attributed either to the Bølling or to the pre-Bølling periods (Cordy, 1994). In the case of the Bølling, the population would then represent a relict population, trapped by temperate climatic conditions, and that may have survived, isolated, for some time before its extinction and the disappearance of the collared lemming from all Western Europe.

5. Conclusion

In conclusion, the shape of the first lower molar of the collared lemming is highly variable and follows temporal and geographical trends that might relate to the different migratory pulses documented from ancient DNA haplotypes. Whereas each pulse appears to be recorded in shape, their effect is quite small compare to the large variation existing at any one time; morphotype proxies of migratory events could not be identified. Dispersal events led to some differentiation according to the distance from the core population and to local divergence on the range margin, with genetic drift as the most likely process.

Author contributions

Conceptualization, S.M., A.R. and N.N.; Methodology, N.N.;

Formal analysis, N.N.; Investigations and Data Curation, S.M.; Writing—original draft preparation, S.M., A.R., and N.N.; Writing, Review and Editing, S.M., A.R., N.N., E.D., N.S., A.S., O.G., A.N., A.L.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.quascirev.2019.105886>.

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