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Surviving in the High Arctic: dental variation in a casually introduced population of *Microtus rossiaemeridionalis* (Arvicolinae, Rodentia) on Svalbard

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Abstract

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A human-mediated invasion of a temperate rodent *Microtus rossiaemeridionalis* on the High Arctic Archipelago of Svalbard in the first half of the 20th century provides an opportunity to explore extent and rate of morphological divergence over decades of isolation. We studied dental size and morphology in 124 voles captured on Svalbard (Spitsbergen) in 1997–2005 and compared the data to mainland conspecific populations across northern Eurasia. Both dental and cranial sizes in the Svalbard population fall within the limits of natural variation of the species. Dental morphology suggests that the population experiences strong effects of isolation as indicated by the significant increase in the frequency of rare dental morphs, possibly caused by inbreeding. No evidence for directional shift towards increased or decreased complexity of the morphotype dental patterns is revealed. Although the population on Svalbard is phenotypically different from the mainland populations (due to increased frequency of rare morphs), those differences are not enough to support the idea of initial rapid evolution related to colonization. The limited spatial extent and environmental homogeneity of suitable habitats on the island allowed the species to initially multiply but not to diversify so that the species exhibits phenotypic conservatism but suffers the consequences of small population size.

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Introduction

Since Darwin, islands have been one of the most popular models for the study of evolution (e.g. Mayr 1967; Berry 1996). Both theory and empirical data suggest that island mammals evolve at faster rates than their mainland congeners and significant phenotypic differences between island and mainland conspecific populations may occur over a few decades of isolation (e.g. Millien 2011).

The sibling vole, *Microtus rossiaemeridionalis* Ognev, 1924 (= *M. levis* or *M. epiroticus*), is a temperate arvicoline species of rodent undergoing significant range expansion via casual introductions by humans (Sokolov and Bashenina 1994). The natural continuous part of the species' distribution area lies

approximately between 60–39°N and 30–60°E, whereas the introduced populations are known as far north as 78°10'N (Yoccoz and Ims 1999) and east as 140°13' E (Tiunov *et al.* 2013).

The population of *M. rossiaemeridionalis* on the High Arctic Archipelago of Svalbard (78°10'N, 15°16'E) represents the northernmost point of the species' occurrence. The population is thought to have originated from animals unintentionally introduced by Russian supply ships from the region around St. Petersburg, Russia, between 1920 and 1960 (Fredga *et al.* 1990; Yoccoz and Ims 1999). It is spatially confined to a relatively small area along the coastal line of Isfjorden on the biggest island of the Svalbard archipelago (Spitsbergen) and is completely isolated from the mainland

populations for at least 50 years providing a unique opportunity to explore the effects of isolation on phenotype under severe environmental conditions far beyond the species' natural range.

The sibling vole, *M. rossiaemeridionalis*, belongs to the group of species known as common voles *sensu lato* [so-called arvalis group in the genus *Microtus* (e.g. Meyer *et al.* 1996)], the adaptive radiation of which has been characterized by a high rate of speciation associated with relatively low rate of phenotypic divergence. Along with the process of cryptic species formation and dispersal throughout a substantial part of mainland Eurasia, cases of relatively rapid morphological divergence without achieving reproductive isolation are known for island populations of some members of the 'arvalis' group, namely for *M. arvalis* on islands in the Atlantic Ocean (Heim De Balsac and Lamotte 1951; Corbet 1986; Cucchi *et al.* 2014). In particular, molar gigantism and development of specific dental morphology in *M. a. orcadensis* is shown to be a result of the initial rapid evolution after colonizing the Orkney Islands about 5000 years ago (Cucchi *et al.* 2014). An analysis of the Svalbard population of *M. rossiaemeridionalis* from the standpoint of microevolution is of particular interest given both the ecological and evolutionary aspects of the relatively recent invasion event. In this study, we ask the following questions:

Is the island population of *M. rossiaemeridionalis* on Svalbard phenotypically different from mainland conspecific populations? And if so, does the population follow the island rule, according to which small mammals become bigger on islands? Does the population show any change in the pattern of phenotypic variability compared to the mainland populations, which might be interpreted in terms of microevolution?

Among a wide variety of phenotype characteristics, we chose to focus on molar teeth because they represent a

traditional model for revealing the patterns of variation and evolution in arvicoline rodents. Molar morphology reflects trophic specialization and allows for interpreting phylogenetic affinities within and among populations and species (e.g. Borodin 2009). Molar size reflects body size and might be used as a proxy for tracking body length or body mass distributions (e.g. Martin 1996). A number of studies have been performed to reveal the patterns of dental variability in *M. rossiaemeridionalis* throughout the main part of the continuous range and in some of the invaded areas in the mainland Eurasia (Malygin 1983; Peskov and Tsudikova 1997; Markova *et al.* 2010; Tiunov *et al.* 2013); however, no data are available on dental variation in *M. rossiaemeridionalis* on islands.

This study aims to describe dental phenotypic variation in the introduced island population of *M. rossiaemeridionalis* on Svalbard and to evaluate the effects of isolation on dental size and morphology by comparing the population on Svalbard with mainland conspecific populations from different parts of the present-day range of the species.

Materials and Methods

Specimens and samples

The Svalbard data set included skulls of 124 individuals of *M. rossiaemeridionalis* caught in 1997, 1999, 2001–2005 within an area of <1 km² by the abandoned mining town Grumant on the south-east coast of Isfjorden (west Spitsbergen, Svalbard, Fig. 1). Trapping was performed on fixed trapping grids (see Stien *et al.* 2012 for the protocol of trapping). Published data on 19 individuals captured in Barentsburg and Colesdalen in 1985–1987 (Bolshakov and Shubnikova 1988) were also taken into account when considering morphotype dental patterns.

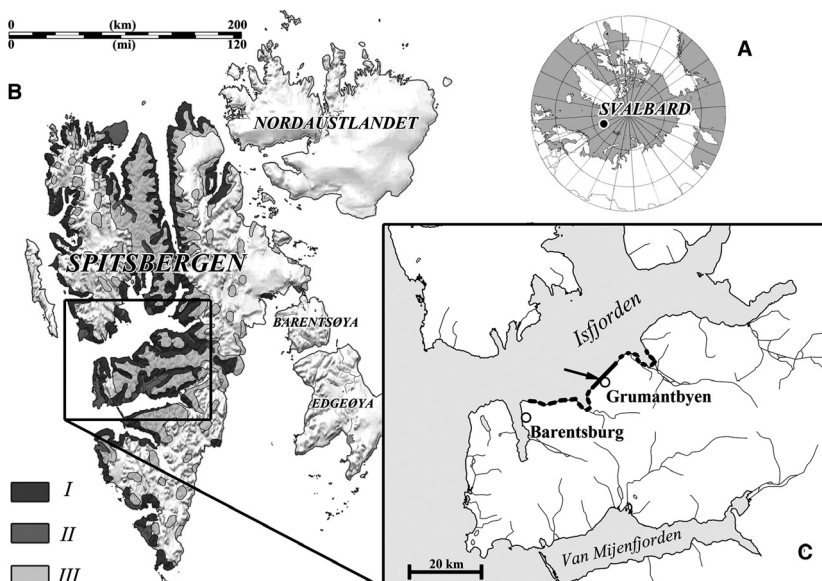


Fig. 1—Study area location maps. (A) An azimuthal projection of the North Pole showing the situation of the Svalbard archipelago. (B) Position of the study area on a map of Svalbard showing the patchy pattern of vegetation on the island of Spitsbergen. I–III – vegetation types 1–15 from <http://www.arcticsystem.no/en/arctic-inc/vegetation.html>: I – dry and mesic vegetation types (1–4, 8–9); II – wetland vegetation types (5–7, 10–12), III – polar deserts (13–15). (C) Distribution of *M. rossiaemeridionalis* on Spitsbergen and the sampling locality. Contour lines indicate persistent occurrence (thick solid line) and distribution in peak vole years (dashed line) after Fuglei *et al.* 2008. The arrow points to the sampling locality (see Stien *et al.* 2012 for the protocol of trapping).

Table 1 Samples and types of material used for comparative analysis (Image sets – collection of digitized images of molars, Skulls – complete skulls) and deposition of specimens (ANHM – Agder Natural History Museum, Agder, Norway, MSU – Moscow State University, Moscow, Russia, ZIN – Zoological Institute RAS, Saint-Petersburg, Russia, IPAE – Institute of Plant and Animal Ecology, Ekaterinburg, Russia)

No	Sample	Coordinates N/E	Type of material	Deposition of specimens	Number of m1/M3	
					Total non-juveniles	Non-juveniles with 100% mature skull
1	Svalbard	78°11′/15°08′	Skulls	ANHM	248/248	54/54
2	Armenia (Aygeyard)	39°57′/44°36′	Image set	MSU	8/8	4/4
3	Volgograd reg.	48°41′/44°28′	Image set	ZIN	12/12	2/2
4	Belgorod reg.	50°36′/36°36′	Image set	MSU	16/16	4/4
5	Voronezh reg.	51°26′/40°33′	Image set	MSU	25/24	3/3
6	Orenburg reg.	52°53′/53°22′	Image set	IPAE	20/18	4/4
7	Bashkortostan (Kinzebulatovo)	53°24′/56°11′	Skulls	IPAE	18/18	12/12
8	Moscow reg. (Zvenigorod)	55°44′/36°51′	Image set	MSU	50/53	13/13
9	Mari El (Yoshkar-Ola)	56°38′/47°52′	Skulls	IPAE	54/54	12/12
10	Ekaterinburg	56°50′/60°35′	Skulls	IPAE	66/60	8/8
11	Sverdlovsk reg. (Bainy)	56°42′/62°08′	Skulls	IPAE	114/114	8/8
12	S.-Petersburg (Pushkin)	59°43′/30°25′	Image set	ZIN, MSU	70/70	11/11
13	Yaroslavl' reg.	57°37′/39°51′	Image set	MSU	16/–	5/–

Comparative materials from 12 mainland populations included skulls (Table 1, Skulls) or collections of digitized images of the tooth rows (Table 1, Image sets). Published data on dental variability in mainland Eurasia (Markova *et al.* 2010) and in the occasionally introduced conspecific population in the Russian Far East (Tiunov *et al.* 2013) were also considered. Both right and left molars of the same individual were included in the analyses.

Metric characters

Dental measurements (maximal length and width of the occlusal surface, Fig. 2) were taken using the programs TPSdig and ScionImage from digitized images obtained from a binocular microscope with a Nikon CoolPix digital camera. The first lower molars (m1) were measured for each sample listed in the Table 1, and both m1s and M3s were measured for the Svalbard sample. Cranial measurements (condylobasal length) were taken for skull samples (Table 1, skulls) using an electronic digital calliper. Each measurement was taken twice and then averaged to reduce the effect of random measurement error. The differences between repeated measurements did not exceed ± 0.02 mm for teeth and ± 0.12 mm for skulls.

Morphotype dental patterns

Occlusal patterns of the lower first (m1), upper second (M2) and third (M3) molars are analysed using a morphotype-based approach. Among a variety of morphological methods, this approach is chosen because (i) it enables interstudy comparability of results when the morphotypes are defined in the same way, (ii) because of the heritability of particular dental

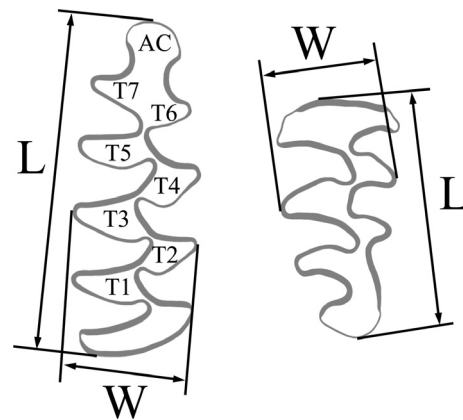


Fig. 2—A scheme for measuring the length (L) and width (W) of the molars m1 (left) and M3 (right) and nomenclature of the m1 occlusal surface: AC – anterior cap; T1–T7 – triangles of the occlusal surface numbered after Van der Meulen (1973).

morphotypes in *Microtus* and (iii) because the principle of morphotype establishment reflects an evolutionary trend towards complication of teeth in Arvicolinae (see Markova *et al.* 2010 for references).

For interstudy comparability, we used the traditional classification of morphotypes for M3 (*simplex*, *typica*, *duplicata* and *variabilis* (*sensu* Rörlig and Börner 1905)) and for m1 (morphotypes I–IV *sensu* Markova *et al.* 2010). Those morphotypes are based on the number of re-entrant and salient angles (and respective dental prisms), and here, we consider them as main morphotypes because they characterize dental variability through the entire range of *M. rossiaemeridionalis* (Markova *et al.* 2010).

To measure dental complexity at individual level, we also used a morphotype ranking approach, which allows us to consider the tooth complexity as a quantitative variable measured by an interval scale (Markova 2014). Both traditional morphotypes and their ranks reflect molar complexity and are based on addition of dental prisms.

Rare morphs and dental abnormalities

Along with the analysis of main morphotypes of cheek teeth, the sample from Svalbard was also checked for the presence or absence of dental abnormalities and rare morphs, which could be found in common voles *sensu lato* with extremely low frequencies: morphs 1–6 (after Jánosy and Schmidt 1960, 1975) and *a-i* (after Markova et al. 2010). To avoid confusion with designations, we call the morph 1 (Jánosy and Schmidt 1975) an *Oec* character because it exhibits a resemblance to *M. oeconomus* in the pattern of confluence between the occlusal elements T5 and AC (*sensu* Van der Meulen 1973).

Individual age of an animal

Here, we used two approaches to establish age classes. The first one was based on percentage of skull maturation (Larina and Lapshov 1974) and included 11 age classes from 0 to 100%. The second approach was based on the occlusal dental pattern and was used when analysing dental morphotypes and complexity. Three dental age classes were established as follows: (i) juvenile individuals with incompletely formed occlusal surface and/or juvenile folding on m1 and/or M3; (ii) young adults with no juvenile characters on all molars; and (iii) adults with definitive outline of the occlusal surface. Criteria to distinguish young and definitive adults were adopted from Nadachowski (1982).

Cranial versus dental age

In the Svalbard sample, incompletely formed occlusal surfaces of M3s were found in animals with immature skulls (0%), and juvenile folding of m1 and/or M3 occlusal outline was found in animals of 10–20% of cranial maturity. The animals with 30–100% mature skulls were regarded as non-juveniles because they normally showed no juvenile enamel folding on their teeth. All animals with 60–100% were definitive adults. No strict correspondence between cranial and dental age within the range of 30–50% of cranial maturity was found so that we used dental age when analysing morphotype dental patterns (with a focus on non-juvenile data sets) and cranial age when analysing metric characters (with a focus either on animals with 100% mature skulls when undertaking the inter-regional comparisons or on animals with 60–100% mature skulls when considering age as a possible source of between-sample differences). Age structure of the samples used to compare ontogenetic patterns is shown in Table 2.

Sex-related variation

Absence of sexual dimorphism in *M. rossiaemeridionalis* was shown for both dental measurements (Markova et al. 2003) and morphotype dental patterns (Markova et al. 2010). Therefore, we do not consider sex as a source of variation within data sets.

Between-year variability

In 1997–2005, the estimated annual vole population size in the sampling area fluctuated between 0 and 286 individuals because of environmental variations such as the rain-on-snow events that cause ground ice (Stien et al. 2012). Rain-on-snow events during warm spells in winter are not uncommon on Svalbard, where the climate is oceanic and rather mild for the

Table 2 Age structure and number of individuals in the samples available for the analysis of both dental and cranial size. See Table 1 for sample numbers. The subsamples included in the ANOVA design are given in bold

Cranial maturity, %	Sample				
	1. Svalbard	7. Bashkortostan (Kinzebulatovo)	9. Mari El (Yoshkar-Ola)	10. Sverdlovsk reg. (Ekaterinburg)	11. Sverdlovsk reg. (Bainy)
0	3	0	0	0	0
10	1	1	0	2	0
20	15	0	0	1	0
30	6	0	0	1	0
40	7	0	1	2	1
50	3	1	2	4	0
60	14	0	3	3	7
70	11	0	7	3	7
80	16	0	3	7	3
90	11	1	2	3	2
100	27	6	6	4	4

Table 3 Condylobasal length of skull and measurements of the occlusal surface of molar teeth (in mm) in *M. rossiaemeridionalis* from Svalbard. Numbers of individuals in each age class are shown in Table 2

Age classes (cranial maturity, %)	Condylobasal length		Length of m1		Width of m1		Length of M3		Width of M3	
	Min/Max	Mean ± SE	Min/Max	Mean ± SE	Min/Max	Mean ± SE	Min/Max	Mean ± SE	Min/Max	Mean ± SE
0	18.62/20.15	19.21 ± 0.48	2.22/2.50	2.34 ± 0.02	0.75/0.94	0.80 ± 0.02	–	–	–	–
10	20.45	20.45	2.46/2.53	2.49 ± 0.04	0.91	0.91 ± 0.002	1.61/1.62	1.62 ± 0.004	0.73/0.78	0.75 ± 0.02
20	19.98/21.74	21.00 ± 0.14	2.42/2.69	2.56 ± 0.01	0.86/1.10	0.95 ± 0.02	1.54/1.78	1.65 ± 0.01	0.61/0.92	0.77 ± 0.02
30	21.23/23.11	21.82 ± 0.29	2.47/2.73	2.59 ± 0.03	0.90/1.12	1.01 ± 0.02	1.58/1.82	1.71 ± 0.02	0.71/0.89	0.82 ± 0.02
40	21.79/23.42	22.32 ± 0.23	2.49/2.74	2.61 ± 0.02	0.93/1.11	1.02 ± 0.02	1.54/1.94	1.77 ± 0.03	0.77/0.94	0.85 ± 0.02
50	21.67/22.90	22.26 ± 0.36	2.43/2.67	2.53 ± 0.04	0.94/1.10	0.99 ± 0.02	1.54/1.79	1.65 ± 0.04	0.74/0.85	0.80 ± 0.02
60	21.48/24.19	23.13 ± 0.21	2.44/2.85	2.63 ± 0.02	0.91/1.10	1.00 ± 0.01	1.56/1.91	1.75 ± 0.02	0.76/0.96	0.85 ± 0.01
70	23.13/25.12	23.71 ± 0.17	2.45/2.84	2.67 ± 0.02	0.96/1.10	1.02 ± 0.01	1.63/1.99	1.81 ± 0.02	0.81/0.98	0.88 ± 0.01
80	23.24/25.09	24.45 ± 0.11	2.60/2.90	2.73 ± 0.01	0.98/1.07	1.04 ± 0.003	1.74/2.01	1.88 ± 0.01	0.84/0.97	0.90 ± 0.01
90	23.67/25.31	24.64 ± 0.13	2.67/2.87	2.76 ± 0.01	1.01/1.10	1.04 ± 0.01	1.72/2.00	1.89 ± 0.02	0.83/0.93	0.88 ± 0.01
100	24.25/26.10	25.25 ± 0.11	2.66/3.13	2.81 ± 0.01	0.96/1.08	1.02 ± 0.003	1.78/2.04	1.91 ± 0.01	0.84/0.96	0.89 ± 0.003

latitude. Unequal sample sizes and highly biased age structure of the yearly subsamples made it impossible to assess between-year variability in dental measurements. Between-year comparisons of the morphotype dental patterns were undertaken for the larger samples of non-juveniles obtained in 2001 and in 2003 (after the year of estimated zero vole abundance in 2002).

Statistical analysis

Statistical analysis relied on programs included in STATISTICA 8.0 package (StatSoft Inc. 2007). We used model I ANOVA (Sokal and Rohlf 1994) to examine the variation in quantitative characters (measurements and dental complexity measured by an interval scale). Post hoc Tukey's HSD test was used to determine which groups among samples have significant differences. Tree building was performed in the Fitch module of PHYLIP 3.695 package (Felsenstein 2004). The index of population similarity in polymorphic parameters ($r_{\text{similarity}}$) and the criterion of identity (I) were evaluated to compare the samples by morphotype frequencies (Zhivotovskii 1979). Standard statistical abbreviations were used according to Sokal and Rohlf (1994): F – Fisher's F statistic, R_S – Spearman's correlation coefficient, P – probability. A criterion of $\alpha = 0.05$ was used to determine significance.

Dental terminology for this study was adopted from Van der Meulen (1973): T – occlusal triangles, AC – anterior cap of m1.

Results

Metric characters

Dental measurements and condylobasal length of *M. rossiaemeridionalis* from Svalbard are shown in Table 3.

Taking into account that the sibling vole exhibits geographic variation in size throughout the species' range and body size in this species decreases with increasing latitude (Malygin 1983), we compare the Svalbard data set with 12 samples encompassing the latitudes from 39°57' to 59°57' N

with respect to molar size (Table 1, Image sets and Skulls) and with 5 samples from 53°24' to 56°50' N with respect to both molar and cranial size (Table 1, Skulls).

To avoid age-related bias, we used only the group of 100% mature individuals to compare m1 size in Svalbard and mainland populations (Fig. 3). The results of one-way ANOVA suggest that the differences between latitudinally arranged samples are significant for both the length ($F_{10;128} = 12.4$, $P < 0.001$) and width of m1 ($F_{10;128} = 7.1$, $P < 0.001$). Tukey's post hoc test shows that the Svalbard sample is significantly smaller than the sample from Aygezard, Armenia ($P = 0.003$ – 0.026) and significantly bigger than the sample from Kinzebulatovo, Southern Urals ($P < 0.001$) with respect to both length and width of m1.

Among the samples arranged by latitude, the closest to the Svalbard sample with respect to m1 length and width is the latitudinal sample from about 56°N, which includes the pooled samples 9–11 from the Table 1. Materials available for analysis allowed us to examine the variation in size that was due to differences among those samples and among age classes from 60% to 100% of skull maturity using model I ANOVA. The first-order interaction terms were tested for sample-related differences in the patterns of ontogenetic variation. The results suggest that differences among samples ($F_{3;270} = 48.8$ – 52.9) and among age classes ($F_{4;270} = 10.4$ – 11.2) as well as the interaction terms ($F_{12;270} = 4.4$ – 4.7) are statistically significant ($P < 0.001$) for all measurements (m1 length and width, condylobasal length). Diagrams (Fig. 4) show that the differences between the Svalbard sample and the mainland samples are the most clearly observed when comparing condylobasal length. For molar size, those differences are less pronounced but show the same trend towards the higher values in the Svalbard sample.

Morphotype dental patterns

Main morphotype frequencies of m1 and M3 in the samples obtained in 1997, 1999, 2001–2005 are shown in Table 4. M2 molars exhibit no additional elements so it was not

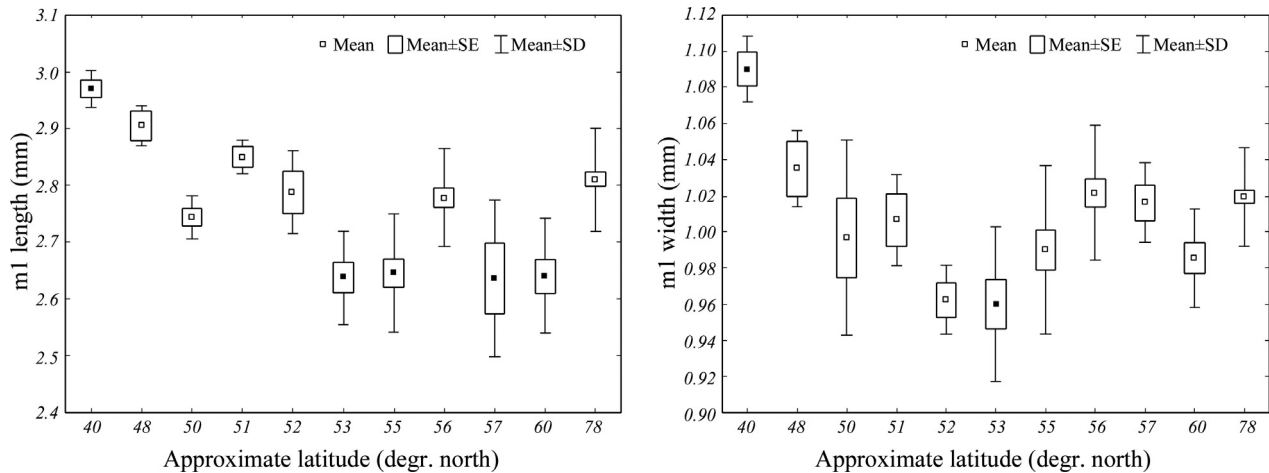


Fig. 3—Geographic variation in tooth size in *M. rossiaemeridionalis* along the latitudinal gradient assessed for individuals with 100% mature skulls. The samples from Table 1 are arranged in ascending order of latitude with pooled data from 56°N (Table 1, samples 9–11); the means, which differ significantly from the Svalbard sample, are marked with black squares.

included in the Table 4. The most typical occlusal surface patterns of M3 and m1 are shown on Fig. 5.

The index of population similarity ($r_{\text{similarity}}$) and criterion of identity (I) were used to evaluate significance of the between-year and between-population differences of the main m1 and M3 morphotypes.

Between-year comparisons of the main morphotype structure in the Svalbard population (2001 vs. 2003) are undertaken for the larger samples (number of teeth in the non-juvenile group ≥ 30). The frequencies of m1 morphotypes differ significantly ($r_{\text{similarity}} = 0.952$, $I = 10.9$, $df = 3$, $P = 0.012$) because of slightly increased number of complex morphotypes in 2003. The frequencies of M3 morphotypes do not differ ($r_{\text{similarity}} = 0.933$, $I = 1.8$, $df = 3$, $P = 0.615$). However, the frequencies of the complexity ranks 1.5, 2.0, 2.5, 3.0 within the morphotypes *typica* and *duplicata* are different between the years ($r_{\text{similarity}} = 0.946$, $I = 14.5$, $df = 3$, $P = 0.002$) because of the relatively higher ranks of M3 complexity in 2003.

To compare the main morphotype structure of the Svalbard population with the mainland populations, we used both the comparative data set listed in Table 1 and the published data (Peskov and Tsudikova 1997; Markova et al. 2010; Tiunov et al. 2013). The complete list of comparative data is given in the Appendix. The representative samples ($N \geq 30$) are used to construct an additive unrooted tree based on both m1 and M3 morphotype frequencies (Fig. 6). Although the samples obtained on Svalbard in 2001 and 2003 differ from one another, they are similar to the sample from the vicinities of St. Petersburg.

Comparison of complexity ranks in Svalbard and mainland populations is undertaken for the data set listed in Table 1. The absolute values of average dental complexity (for both m1 and M3) revealed on Svalbard (Fig. 7, 78°N) are quite similar to those in the sample from vicinities of St. Petersburg (Fig. 7, 60°N).

Rare morphs and dental abnormalities

Of 16 possible rare morphs (a–i, 1–6), the two was present in the Svalbard population. One female exhibited slightly expressed h morph on the left molar (Fig. 5, Id 109). Another rare morph (the *Oec* character) was found to be more frequent (Fig. 5, Id 5 and Id 102).

On Svalbard, the *Oec* character is revealed on average in 15% of m1s, and in the years when the number of captured animals exceeded 20, the frequency of that morph varies from 13 to 59% (Table 4). This character is often found on the molars with the broad confluence between T1 and T2 (Fig. 5); and the two characters are positively correlated in the Svalbard data set ($R_S = 0.25$, $P < 0.001$).

Previous results showed that the *Oec* morph could be revealed in natural populations of *M. rossiaemeridionalis* in the Urals with low frequency, not higher than 3% (Markova and Borodin 2005). Among the comparative data sets (Table 1), single specimens with the *Oec* character are found in samples 1, 3, 5–7, 10–13.

Although no cheek tooth abnormalities was found in *M. rossiaemeridionalis* from Svalbard, single adult individuals (90–100% of cranial maturity) exhibited extremely long incisors, which sometimes led to malocclusion.

Discussion

The evidences concerning the size of *M. rossiaemeridionalis* on Svalbard compared to the mainland conspecifics had long been rather contradictory. Corbet (1986) mentioned, as a reference to Alendal (1977), that a normal, small form of common vole *sensu lato* is present on Svalbard. At the same time, a comparison between the Svalbard population and the mainland conspecifics from Finland showed that adult body masses are much greater on Svalbard than in Finland, possibly

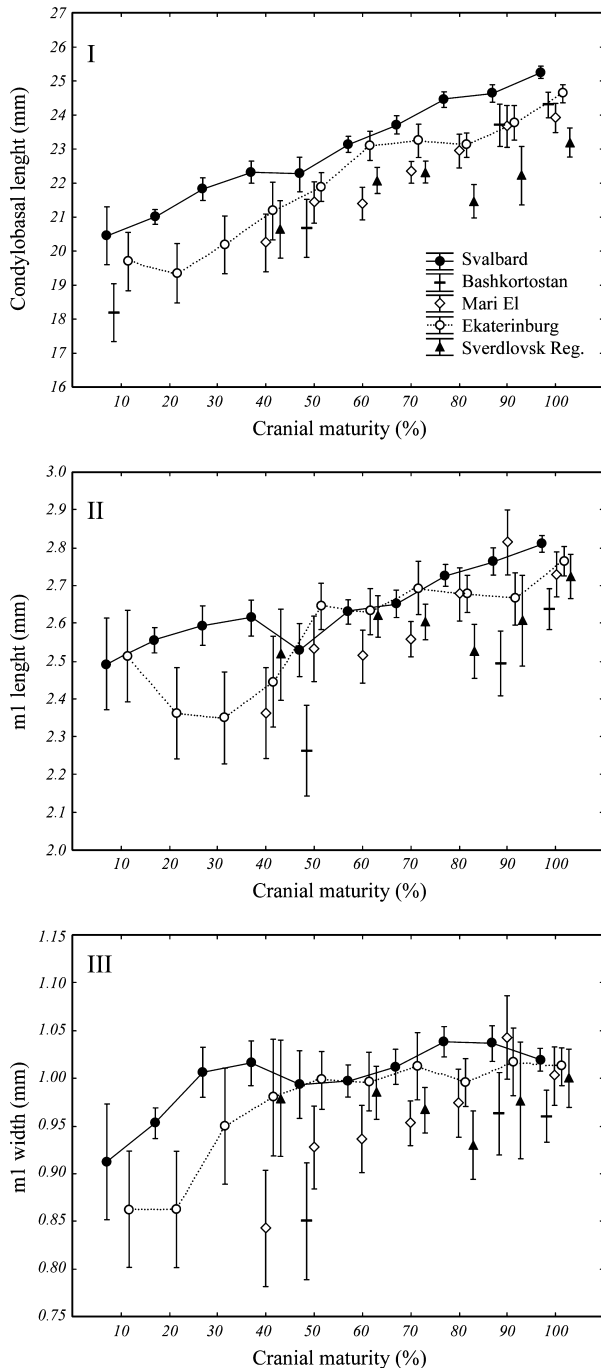


Fig. 4—Mean values of condylobasal length (I), m1 length (II) and m1 width (III) in samples 1, 9–11 used to assess age as a possible source of intersample differences. Number of individuals and age classes included in the ANOVA design are given in Table 2. Vertical bars denote 95% confidence intervals.

due to a phenotypic response to the cold arctic climate (Yoccoz and Ims 1999). Our data clearly suggest that mean values of m1 length and width in the Svalbard sample, as well as the

condylobasal length fall within the range of geographic variation of the species. However, if we take into account the pattern of geographic variation known for the species (certain decrease in body size with increasing latitude (Malygin 1983), we should conclude that the animals from Svalbard are slightly bigger than their conspecifics occurring in the northern parts of the species' distribution range. The most reliable explanation to that is that the Svalbard and mainland populations at the latitudes of 56–60° north are subjected to different climatic stress factors. One of the most probable reasons for that is the specificity of climate on Svalbard (relatively milder winters compared to the Eurasian mainland at 56–60° north and the presence of extreme climatic events which determine the abundance of the species).

First data on dental morphotypes in *M. rossiaemeridionalis* on Svalbard are dated back to 1985–1987 when Bolshakov and Shubnikova (1988) obtained 19 individuals from Barentsburg and Colesdalen. The animals had 'usual morphotype' of m1 (here it is mentioned as morphotype I) and morphotype *typica* on M3. Although Bolshakov and Shubnikova provide no frequencies for particular morphotypes, the combination of main morphotypes remains principally the same on Svalbard from 1985 to 2005: morphotypes I and *typica* are overdominating (respectively, 87–95% and 86–100% of the m1 and M3 morphotype spectrum in different years). Among M3 morphotypes, *duplicata* is a reserve morphotype, the frequency of which varies among years (in the studied samples it does not exceed 12%). This could be regarded as a normal pattern of variability in the sibling vole (Markova et al. 2010).

Between-year comparison of the morphotype dental patterns in the Svalbard data set suggests that the sample obtained in 2003 is more variable than the one from 2001 and shows slightly (though significantly) increased number of complex molars. It might be due to the population dynamics described for the sampling area (Stien et al. 2012). The year of zero vole abundance was 2002, so the increased variability in 2003 might be due to population growth related to recolonization of the sampling area.

Regardless of between-year differences, the most similar to the Svalbard population with respect to morphotype structure of both m1 and M3 is the sample from the north-west of Russia (vicinities of St. Petersburg). Although the samples obtained on Svalbard in 2001 and 2003 differ from one another, they are quite similar to the sample from the vicinities of St. Petersburg. These results support the previous ideas about the most probable geographic location of the source population, which has colonized the island of Spitsbergen (Fredga et al. 1990). However, the grouping of samples based on morphotypes (Fig. 6) does not strictly coincide with the geographic location. Moreover, the morphotype I on m1 and *typica* on M3 might be also over-dominating in the samples of sibling vole from central Ukraine (Appendix: Cherkasy, Kyiv and Poltava regions), although those published data are not large enough to adequately compare morphotype frequencies.

Table 4 Main morphotypes of the lower first and upper third molars, according to their respective ranks of complexity, and rare m1 morphs revealed in the Svalbard population of *M. rossiaemerdionalis* over six sampling years

Sampling year	Dental age classes	Number of individuals	Number of teeth assigned to morphotypes/Morphotype frequency*										
			Main m1 morphotypes (complexity ranks)				Rare m1 morph <i>Oec</i>	Main M3 morphotypes (complexity ranks)					
			I (3)	II (4)	III (4)	IV (5)		<i>Simplex</i> (1)	<i>Typica</i>		<i>Duplicata</i>		<i>Variabilis</i> (4)
(1.5)	(2)	(2.5)	(3)										
1997	Non-juvenile (definitive+young)	1	2/–	0/–	0/–	0/–	1/–	0/–	0/–	2/–	0/–	0/–	0/–
1999	Non-juvenile (definitive+young)	2	3/–	0/–	0/–	0/–	1/–	0/–	0/–	3/–	0/–	0/–	0/–
2001	Non-juvenile (definitive+young)	21	42/0.95	2/0.05	0/0	0/0	13/0.59	0/–	27/0.64	12/0.29	1/0.02	2/0.05	0/–
	Young	1	0/–	2/–	0/–	0/–	0/–	0/–	0/–	0/–	0/–	2/–	0/–
2003	Non-juvenile (definitive+young)	82	143/0.87	8/0.05	5/0.03	8/0.05	22/0.13	0/–	53/0.32	89/0.54	3/0.02	19/0.12	0/–
	Young	9	5/–	3/–	2/–	8/–	2/–	0/–	0/–	11/–	0/–	7/–	0/–
2004	Non-juvenile (definitive+young)	3	6/–	0/–	0/–	0/–	3/–	0/–	0/–	6/–	0/–	0/–	0/–
2005	Non-juvenile (definitive+young)	6	12/–	0/–	0/–	0/–	0/–	0/–	1/–	11/–	0/–	0/–	0/–
Total	Non-juvenile (definitive+young)	124	224/0.90	10/0.04	6/0.02	8/0.03	38/0.15	0/–	93/0.38	130/0.53	4/0.02	20/0.08	0/–
	Young	10	5/–	5/–	2/–	8/–	2/–	0/–	0/–	11/–	0/–	9/–	0/–

*Morphotype frequencies in fractions of one are calculated for sample sizes larger than 30 (including right and left molar teeth).

Based on molar morphology, we cannot reject the possibility of convergent similarity between the samples from Svalbard and St. Petersburg. Further genetic studies might clarify this question.

The analyses of main morphotype frequencies and complexity ranks in the Svalbard population of sibling vole reveal no shifts towards simplification or increased complexity of m1, M2 and M3 as compared to the mainland conspecifics. High similarity of morphotype frequencies and complexity estimates between the Svalbard data set and some mainland samples (first of all, St. Petersburg) suggests that the sibling vole occurring on Svalbard retains rather a conservative pattern of dentition.

At the same time, the Svalbard population is different from the mainland ones due to increased frequency of one rare morph – an *Oec* character (13–59%). Single findings of this morph in comparative populations (up to 3%) suggest that this dental phenotype persists within the mainland populations of the species but is kept at a low frequency (not higher than 3%).

Genetic background of the *Oec* character was previously considered in common voles *sensu lato*, namely in *M. arvalis obscurus* (Rakitin *et al.* 2009). Being extremely rare in natural populations, the *Oec* character increased its frequency in laboratory-bred animals. Of 1700 offsprings obtained from four males and 10 females of *M. a. obscurus*, about 9% possessed

this character on m1 (Rakitin *et al.* 2009). The analysis of heritability of this character showed that all individuals with this unusual pattern of m1 originate from one female caught pregnant in the wild. Taking those results obtained on *M. a. obscurus* as an indirect evidence for the heritability of the *Oec* character in common voles *sensu lato*, we can conclude that the increased frequency of this rare morph in the Svalbard population of *M. rossiaemerdionalis* is most probably a result of the founder effect and inbreeding under conditions of isolation.

Another difference of the Svalbard population from the mainland ones is the presence of individuals with extremely long incisors. This abnormality is caused by low rates of a tooth wear compared to its growth and is usual for hypselodont voles living in captivity; however, it has not yet been revealed in natural population of the sibling vole. The presence of individuals with extremely long incisors, which sometimes lead to malocclusion, appears to be related either to high survival rates known in the sibling vole population on Svalbard (Yoccoz *et al.* 1993; Henttonen *et al.* 2001) or to a possible dietary shift towards the less abrasive diet. The sibling vole on Svalbard is confined to the highly fertilized bird cliffs covered by luxuriant herbaceous vegetation. According to observations in the wild, the sibling vole on Svalbard feeds on monocots, for example *Alopecurus* (Ims & Yoccoz, personal communication). Monocots also constitute a substantial

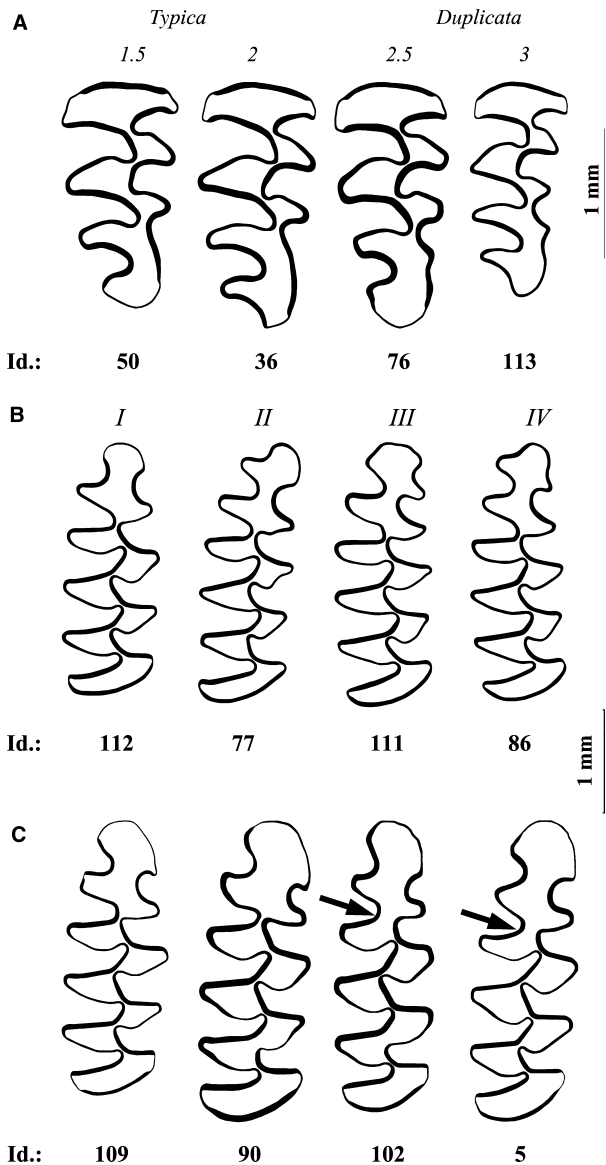


Fig. 5—Enamel outlines of the occlusal surface of the upper third (A) and lower first (B–C) molars in *M. rossiaemeridionalis* on Svalbard. (A) Left M3s and correspondence between traditional morphotypes (*typica*, *duplicata*) and dental complexity ranks (1.5–3). (B) Right (Id 86, 111, 112) and mirrored left (Id 77) m1s assigned to the main morphotypes I–IV. (C) Right (Id 5, 102) and mirrored left (Id 5, 109) m1s showing the rare morphs: Id 109 – m1 bearing a small fold with the enamel-free apex on the anterior edge of T7; Id 90 – m1 showing the broadly confluent T1 and T2; Id 102 – m1 showing the broadly confluent T1–T2 and T5–AC; Id 5 – m1 with the broadly confluent T5–AC. The broad confluence between T5 and AC (*Oec* character) is indicated by arrows. Id – identification numbers of individuals.

portion of the species diet in the mainland populations (Sokolov and Bashenina 1994). Low rates of tooth wear might be determined by decreased silica content of the food plants on Svalbard which are little exposed to herbivory.

It is an open question how much does the rate of tooth wear contribute to the manifestation of the *Oec* character in the Svalbard population. None of the individuals with overgrown incisors exhibit the *Oec* character, so that the broad confluence between T5 and AC is not a result of malocclusion. Knowing the evolutionary patterns of dental variation in Arvicolinae, the cheek teeth with broadly confluent triangles show presumably lower abrasion resistance and appear to be less adapted to high-abrasive diets than those with the occlusal triangles completely isolated by diagonally oriented enamel ridges because the diagonal alignment of enamel ridges reinforces the efficiency of grass processing in Arvicolinae (e.g. von Koenigswald 1980). Both the increased frequency of the *Oec* phenotypes and the presence of animals with overgrown incisors might hypothetically reflect a dietary shift towards a softer diet in the Svalbard population. Thus, our results raise a question whether the increased frequency of molars with broadly confluent elements of the occlusal surface is adaptive under environmental conditions on Spitsbergen. And if it is, whether genetic or plastic adaptation is driving variation in m1 morphology within this population of the sibling vole.

Conclusion

Is the island population of M. rossiaemeridionalis on Svalbard phenotypically different from mainland conspecific populations?

Yes, the Svalbard data set is different because of the increased frequency of rare morphs, which might suggest the presence of a founder effect and subsequent inbreeding. Genetic drift in a small population might be a sole factor that shaped the patterns of dental variability in *M. rossiaemeridionalis* on Svalbard or it might interact with natural selection. Assessment of the relative roles of random genetic drift, natural selection and phenotypic plasticity requires further studies.

Does the population follow the island rule, according to which small mammals become bigger on islands?

With respect to dental and cranial size, the population falls within the limits of natural variation of the species throughout the mainland Eurasia. Both dental and cranial size characters provide no evidence to undoubtedly support the island rule.

Does the population show any change in the pattern of phenotypic variability compared to the mainland populations, which might be interpreted in terms of microevolution?

From an evolutionary and ecological standpoint (Shvarts 1977), a microevolutionary event is related to an irreversible change of the population's genetic structure. In our study, we found evidence for the non-directional homoeostatic changes in the population structure (as indicated by the main morphotype dental patterns) and for directional change towards increased frequency of rare dental morphs.

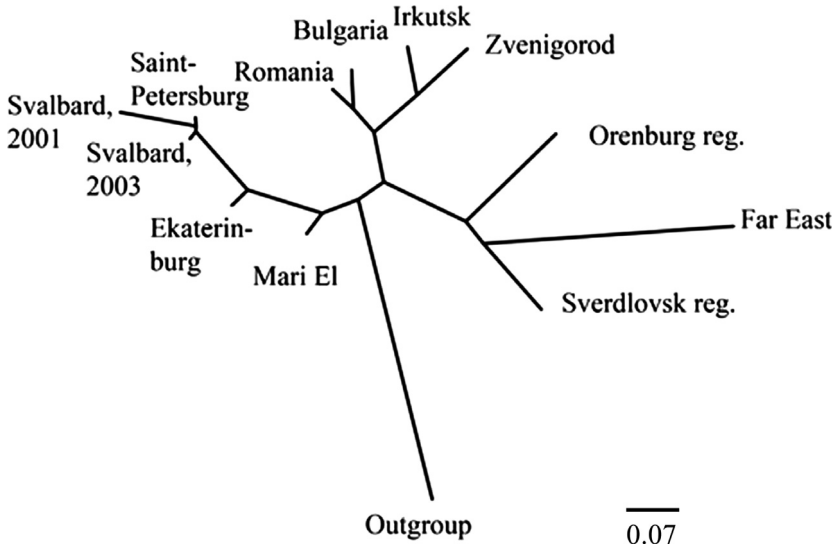


Fig. 6—Fitch-Margoliash unrooted tree obtained from dissimilarity matrix based on m1 and M3 morphotype frequencies in *M. rossiaemeridionalis* from Svalbard (samples taken in 2001 and 2003) and from 10 conspecific mainland populations, with a speculatively selected out-group (a population of *M. arvalis arvalis* showing the simplest pattern of dentition, which was previously revealed in modern common voles *sensu lato* (Markova et al. 2010, sample 21). Details and citations relevant to comparative populations of *M. rossiaemeridionalis* are given in Appendix. All samples comprise no juveniles; $N \geq 30$.

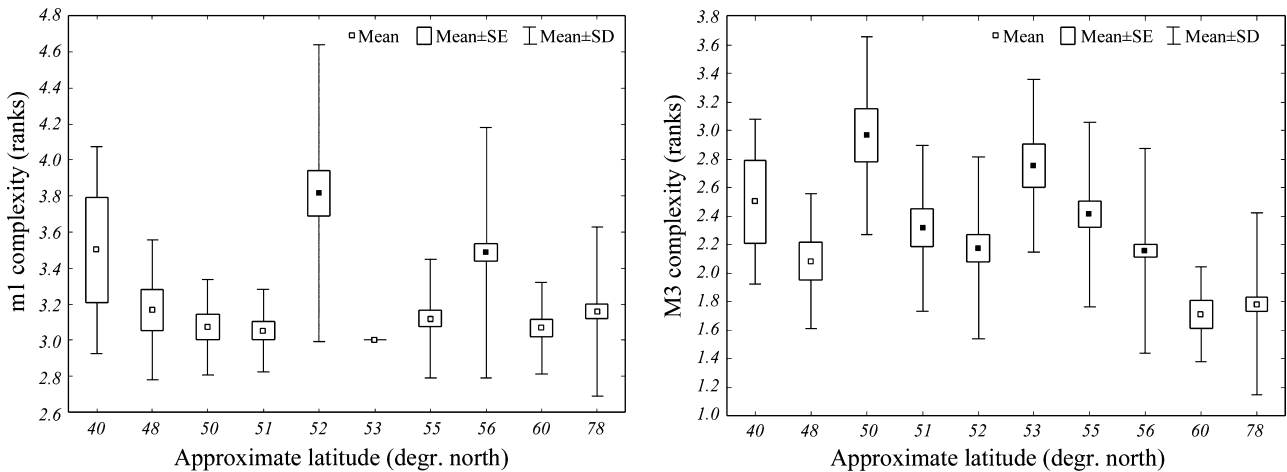


Fig. 7—Geographic variation in dental complexity in *M. rossiaemeridionalis* along the latitudinal gradient assessed for the non-juvenile data sets. The samples from Table 1 are arranged in ascending order of latitude with pooled data from 56°N (Table 1, samples 9–11); the means, which differ significantly from the Svalbard sample, are marked with black squares.

Given a substantial genetic background of the characters under study, the population of sibling vole on Svalbard might have been passed into the stage preceding a microevolutionary event, but the differences between the Svalbard and mainland populations could not yet be regarded evolutionary significant. Although the population on Svalbard is phenotypically different from the mainland populations (due to increased frequency of rare morphs), those differences are rather minor and not enough to support the idea of initial rapid evolution related to colonization of the island. Invasion of a vacant niche on Svalbard allowed the sibling vole to initially multiply but not to diversify morphologically and ecologically because of the limited spatial extent and environmental homogeneity of suitable habitats.

Some ecological and evolutionary perspectives

Despite the extreme northern location of the habitats occupied by *M. rossiaemeridionalis* on Svalbard, the environmental circumstances allow the species to keep the size and morphology similar to the mainland conspecifics for at least 50 years. At the same time, the Svalbard population in the wild exhibits some morphological features of a captive population, such as the increased frequency of rare morphs and the presence of animals with overgrown incisors. Taken together, the results allow us to interpret the invasion of *M. rossiaemeridionalis* on Svalbard as the case of an ecologically subsidized survival of a temperate vole species in the High Arctic. Among the factors, which possibly serve as ecological subsidies, we should mention the impact of warm Atlantic streams on the conditions of

wintering (energetic subsidies) and the luxurious vegetation under seabird colonies (diet subsidies).

The absence of conditions for adaptive radiation on the island of Spitsbergen might be the main reason why the sibling vole has remained undiverged from the mainland conspecifics with respect to size and tooth morphology. Comparing the case of *M. rossiaemeridionalis* on Svalbard with the case of *M. arvalis orcadensis* on the Orkney Islands (Cucchi *et al.* 2014), we can hypothesize that the initial rapid evolution is only possible under favourable environmental circumstances, which promote the invader spread through a principally new habitat, or a variety of habitats. In contrast to the Orkney vole, which has diverged in several populations under the conditions of temperate climate, the ecologically subsidized survival of the sibling vole on Svalbard and limited spatial extent of suitable habitats might have favoured the phenotypic conservatism of the population. Even though the most of mammalian lineages, including rodents, exhibit the tendency towards size increase over the course of time (e.g. Baker *et al.* 2015), we suppose that the driving force for this process is not the time itself but the possibility to diversify. In this context, the case of *M. rossiaemeridionalis* on Svalbard provides the evidence for initial phenotypic stasis under the conditions of severe environment and limited extent of suitable habitat.

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