



The effects of population bottlenecks on dental phenotype in extant arvicoline rodents: Implications for studies of the quaternary fossil record

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ABSTRACT

The consequences of population bottlenecks for dental phenotypes are studied in Arvicolinae, a sub-family of cricetid rodents widely used as a proxy of environmental change and an index group for relative dating and correlation of the Quaternary deposits throughout the Holarctic. Comparative morphological analysis reveals similar phenotypic shifts in populations of extant *Dicrostonyx*, *Lemmus*, *Myopus*, *Microtus* surviving bottlenecks in captivity or in the areas favouring genetic drift (coastal zones and islands, patchy landscapes in the mountainous areas, declining peripheral populations). Six to ten founders is enough for an isolated population to reproduce the full range of species-specific variability in fitness-related characters (crown complexity and occlusal regularity) during the first two generations, while the average values of both characters exhibit founder dependence. When lasting longer than 3 generations, bottlenecks increase diversity owing to 1) the accumulation of rare traits of complexity and regularity inherited from the founders and 2) inbreeding impacts (the loss of advanced morphology and appearance of extra elements in places of the lophs and cusplets of an ancestral cricetid molar). Founder-related and inbreeding-induced simplifications of dentition might potentially lead to biochronological discrepancies in the fossil record of Arvicolinae. To detect possible biases in biochronological data, the phenotypic markers of close breeding are identified. Application of the results to the fossil record of collared lemmings from the north of West Siberia allows hypothesising the periods of increased genetic drift in the ancestral forms of *Dicrostonyx* in the late Middle Pleistocene and in the early Late Pleistocene.

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1. Introduction

The Quaternary fossil record offers a variety of biological proxies to indirectly assess past climate and landscape dynamics and provides direct evidence to write up evolutionary history of living organisms by tracing them back to direct ancestors. Although the resolution of the fossil record is limited by its incompleteness resulting from the organismic, ecological, stratigraphic factors, and sampling bias (Kemp, 1999; Foote and Sepkoski, 1999; Dunhill et al., 2012), the most widespread and abundant taxonomic groups may

serve as the model objects to address those limitations and to develop the approaches to overcome them. In this study, we consider bottleneck effects in extant species of arvicoline rodents in order to assess possible contribution of small population size effects to the patterns of phenotypic variation in one of the most-in-demand groups of small vertebrates among the biological proxies used in the Quaternary paleoecology and biostratigraphy across the Holarctic. Knowing that the fossil record is incomplete and extinct forms are more readily discovered when they are widespread and abundant, we test the possibility of detection of the periods of small population size based on the phenotypic data available in Quaternary fossil assemblages.

The concept of population bottlenecks as the events leading to drastic decreases in population size and inducing stochastic loss of

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genetic diversity has become extremely popular in biological sciences (Manica et al., 2007; Amos and Hoffman, 2010; Palkopoulou et al., 2013; Ingram et al., 2015; Vogwill et al., 2016). Both theoretical and empirical researches suggest that abruptly decreasing genetic diversity favors recombination of alleles that are identical by descent but surprisingly little is known about the consequences of naturally occurring bottlenecks for fitness related phenotypic traits. The problem of small population size and inbreeding has been considered primarily for genus *Homo* and species involved in human activity (e.g., Coppinger and Smith, 1983; Manica et al., 2007). However, contribution of naturally occurring bottlenecks to phenotypic evolution under natural selection remains elusive. Can we trace back the periods of stochastic loss or fixation of fitness-related traits in the fossil record or such stochastic processes should be considered negligible compared to the selection-driven trends in the evolution of species and higher taxa? To address this question, we perform a study on the subfamily Arvicolinae (Rodentia: Cricetidae), a group of small mammals stemmed from the ancestral cricetid stock in the Miocene and experienced several waves of adaptive radiation across the Northern Hemisphere.

During the Quaternary, the rates of phenotypic evolution in arvicoline rodents have been accelerated in response to climatic and environmental changes. Arvicolines have gained a number of structural adaptations in dentition reflecting their specialization for high-fiber food processing (high-crowned cheek teeth with cusps transformed to prisms, and flat occlusal surfaces with the enamel cutting edges), and an overwhelming majority have developed an increased number of dental prisms to improve the efficiency of grating. Gradual increases in the complexity of molars from the ancestral genera to the present-day taxa in the most widespread and abundant arvicoline lineages have become a high resolution proxy for the Quaternary biochronology and biostratigraphy in both Eurasia (e.g., Sutcliffe and Kowalski, 1976; Nadachowski, 1982; Tesakov, 2004; Zazhigin, 2004; Maul and Markova, 2007; Lozano-Fernández et al., 2014) and North America (e.g., Bell, 2000; Martin, 2004; Martin et al., 2011). When used for biochronological and biostratigraphical purposes, the phenotypic rearrangements of arvicoline dentition over the course of time have always been regarded as the irreversible trends. However, the evidence grows that dental characters might exhibit a tendency to reversals towards ancestral character states under experimental conditions (Kangas et al., 2004) or in captive (Markova and Smirnov, 2018) and translocated populations of arvicolines (Markova et al., 2019).

This study aims to reveal general and species-specific impacts of drastic reduction in population size on dental phenotype in wide-ranging North-Eurasian arvicoline species, and to identify the applicability of dental phenotypic characters as potential makers of severe population bottlenecks in the Quaternary fossil record.

2. Materials and methods

The study is performed on the genera *Ondatra*, *Lemmus*, *Myopus*, *Dicrostonyx*, and *Microtus* that represent different waves of the arvicoline radiation and comprise the widespread recent species, the ancestors of which are known as biochronologically important taxa. We consider arvicoline populations, natural and artificial, living and extinct, as the main object of this study. The complete list of samples and relevant publications are shown in Supplementary Table A.

For recent species, taxonomic names are provided following Abramson and Lissovsky (2012), with minor modifications. We designate two karyotypic forms of *M. arvalis* – *arvalis* and *obscurus* – as *M. (arvalis) arvalis* Pallas, 1778 and *M. (arvalis) obscurus* Evermann, 1841 to show their high yet incomplete differentiation and

to avoid misunderstanding when considering the data from different regions. By doing so, we accept the interpretation of these forms as semispecies (Lavrenchenko et al., 2009) and follow the rules of the International Code of Zoological Nomenclature (1999) while including the superspecies name, thereafter abbreviated, in parentheses. Taxonomic names for extinct forms are taken from relevant publications (Table A), except for *Predicrostonyx meridionalis* Smirnov et Borodin (1986) first described as *Dicrostonyx meridionalis* (Smirnov et al., 1986) and then reconsidered (Borodin, 2012). Taking into account different interpretations of the genus, we use a tentative generic designation (*Predicrostonyx?* *meridionalis*) allowed by the International Code of Zoological Nomenclature (1999).

2.1. Case studies

Bottleneck events considered in this study differ by their nature, severity and duration. Five case studies (sections 2.1.1–2.1.5) are accomplished in order to answer the following questions. Do natural populations of arvicoline rodents, living and extinct, exhibit phenotypic shifts comparable to those observed in close-bred captive colonies (Markova and Smirnov, 2018) and translocated populations (Markova et al., 2019)? Can we use dental phenotypic traits as markers of past population bottlenecks? Can we recognise the periods of intensified genetic drift in natural source populations contributed to the formation of Quaternary arvicoline assemblages? Can we consider the phenotypic shifts in small populations negligible compared to the evolutionary trends known for the lineages to which the species belong?

2.1.1. Laboratory colonies

Colonies of *Dicrostonyx* and *M. (a.) obscurus* are considered as the fully documented artificial bottlenecks observed in uniform conditions (Gileva and Rakitin, 2006; Rakitin et al., 2009; Markova and Smirnov, 2018). The colonies were maintained to study chromosome variation and dental characters were not considered during breeding experiments. Here, we provide comparisons of dental characters between the two species and among the colonies, natural conspecific populations, and direct ancestral forms. The comparative fossil record of *Predicrostonyx*–*Dicrostonyx* lineage is characterised by the data from the Urals and West Siberia (Supplementary Table A) and by published data on the distribution and dental variation (Hinton, 1910; Guthrie and Matthews, 1971; Sutcliffe and Kowalski, 1976; Nadachowski, 1982; Smirnov et al., 1986, 1999; Borodin et al., 2013; Ponomarev and Puzachenko, 2015; Crégut-Bonnoure et al., 2018). The comparative fossil record of the lineage *Allophaiomys*–*Microtus* sensu stricto and the clade *Allophaiomys* – generic group *Microtus* sensu lato is considered by using published data (e.g., Smirnov et al., 1986; Hir and Venczel, 1998; Tesakov, 2004; Murray et al., 2011; Luzi and López-García, 2019).

2.1.2. Populations of translocated species

Populations passing through human-mediated bottlenecks have been recently studied using the sibling vole, *M. rossiaemeridionalis* Ognev, 1924, as a model object (Markova et al., 2019). The sibling vole has been occasionally introduced to five regions of Northern Eurasia and three of five introduced populations experience significant phenotypic shifts. Here, we consider another invasive species, *Ondatra zibethicus* Linnaeus, 1776 introduced in Sverdlovsk Region, the Middle Urals, in 1930–1935 during the first stage of the all-Russia campaign for muskrat acclimatisation. A total of 247 animals were released in two geographically close sites and the population increased without any admixture until the end of the 1940s. The dataset includes m1s collected from hunters in

1964–1972, during the period of maximum species' abundance and hunting harvest (unpublished archives of the Sverdlovsk Society of Hunters and Fishermen). The samples (loc. 1–4, [Supplementary Table A](#)) represent two local populations in the area of the first introduction and two sites in the conventional contact zone with the population originated from a southern place of introduction. *Pliopotamys meadensis* Hibbard, 1938 (= *Ondatra meadensis* (Hibbard, 1938) sensu [Martin, 2004](#)) is used as a comparative taxon to illustrate approximate amounts of evolutionary change in the lineage (the range of variability is outlined based on the published data ([Hibbard, 1956](#))).

2.1.3. Island populations

Island effects on dental phenotypic variation have been addressed in a previous publication on *M. rossiaemeridionalis* occasionally introduced to the High Arctic Archipelago of Svalbard ([Markova et al., 2016](#)). Here, we use the samples of *Lemmus sibiricus* Kerr, 1792 and *D. torquatus* Pallas, 1778, collected from the birds of prey pellets on the High Arctic islands as a comparative dataset to test for the presence of common phenotypic shifts among island populations of different species with different population histories ([Supplementary Table A](#)). We consider *L. sibiricus* from Wrangel Island (samples collected in 1984 and 2004–2005), the New Siberian Islands, and Bely Island (one-time samples). Populations of *D. torquatus* are represented by one-time samples from Bolshoy Routan and Bely Island. Comparative data on genetic diversity available for *Lemmus* and *Dicrostonyx* occurring on Wrangel Island ([Fedorov, 1999](#)) are used for interpretation of the results.

2.1.4. Natural population cycles in expanding species

We consider population dynamics as a possible cause of bottleneck effects induced by local population declines. Phenotypic variation and its relation to the species' abundance are addressed in two native North-Eurasian species, *Myopus schisticolor* Lilljeborg, 1844 and *M. (a.) obscurus* referred to as recently expanding species based on the demographic models inferred from molecular genetic data ([Fedorov et al., 2008](#); [Sibiriyakov et al., 2018](#)). Morphological samples are collected in the Ural Mountains and adjacent plains ([Supplementary Table A](#)). The obtained results on recently expanding species existing in continuous ranges are compared to extant *M. rossiaemeridionalis* from Svalbard ([Markova et al., 2016](#)), a species with no available habitats to pass to the expansion stage after successful establishment in the restricted area. We combine morphological data with published ([Bobretsov et al., 2005](#); [Markova et al., 2010, 2013](#); [Stien et al., 2012](#); [Yalkovskaya et al., 2012](#); [Bobretsov and Lukyanova, 2017](#)) and unpublished ([Supplementary Table A](#)) estimations of population dynamics for the periods of morphological data collection.

2.1.5. Declining species

We consider range dynamics in a declining species, *D. torquatus*, as a possible cause of phenotypic changes. A severe genetic bottleneck at the Late-Pleistocene – Holocene transition has been documented for this species using molecular genetic data ([Prost et al., 2013](#)). The recent decline in the north of the West Siberia has been observed by the northward shift of the southern range limit during the last decades ([Sokolova et al., 2014](#)). The area of decline is represented in the morphological dataset by locality Kharp (a southern peripheral population existed in 1970s but recently extinct) and the colony Kharp (CK) founded by 6 animals captured in Kharp in 1971. Dental variation across 12 generations of breeding has been previously described ([Markova and Smirnov, 2018](#)). The comparative data on the natural source population is represented by a newly found unpublished collection of pellets taken directly in Kharp in 1971–1972.

2.2. Dental variation

To ensure compatibility of paleontological and neontological approaches, we focus this study on dental phenotypes. Dental nomenclature for arvicolines is adopted from [Van Der Meulen \(1973\)](#) with some modifications and additions summarised in [Appendix A](#). To establish homology with ancestral tooth plans, we use the terminologies proposed for early cricetids ([Fahlbusch, 1964](#); [Reig, 1977](#); [Maridet and Ni, 2013](#)).

To determine enamel microstructures associated with plesiomorphic tooth patterns, the scanning electron microscope TESCAN VEGA3 was used to obtain microphotographs of the specimens with flattened occlusal surface after washing in 2n HCl during 3 s. Enamel types are identified using the criteria defined by [Koenigswald \(1980\)](#).

Among dental variables we consider 1) crown complexity ([Fig. 1, Appendix A](#)) and occlusal regularity of cheek teeth ([Appendix A](#)) as the characters closely associated with fitness ([Markova, 2014](#); [Markova et al., 2019](#)); 2) non-specific extra elements of the occlusal surface in place of the features of an ancestral cricetid tooth plan ([Appendix A](#)), 3) dental phenotypic anomalies arising from experimental modifications of tooth development in rodents ([Kangas et al., 2004](#); [Charles et al., 2009](#); [Cho et al., 2011](#); [Rodrigues et al., 2013](#); [Harjunmaa et al., 2014](#)).

Variables in groups 2–3 are treated as binary yes/no variables. Crown complexity is measured on an interval scale. We calculate the number of fully developed prisms T1–Tn and identify complexity rank for each molar using the interval scale of complexity ranks ([Markova, 2014](#) and Table 1 therein), where the intervals are relevant to the morphogenetic stages and reflect the iterative addition of cusp pairs after the embryonic day E16 ([Jernvall et al., 2000](#)). The correspondence of complexity ranks to the sequence of evolutionary morphotype progression in two arvicoline lineages yielding biochronologically important taxa is shown in [Fig. 1](#). Average complexity of dentition, ACD is a continuous variable calculated for an individual or for a sample as a sum of average complexity ranks of all molars (i.e., average complexity rank of all m1s + average complexity rank of all m2s + average complexity rank of all m3s, and so on for all six molars). To assess occlusal regularity, we use the ordinal variable ACS (the number of incompletely separated dentine fields in the anteroconid complex of the first lower molar) starting from the prisms T4 and T5 ([Appendix A](#)). In contrast to complexity, the regularity might not be measured on an interval scale until the activation/inhibition balance of its development is clarified to develop equally spaced intervals.

2.3. Sources of variation and analysis

The main concern of this paper is to examine the amounts of spatiotemporal variation after the periods of severe population bottlenecks. We focus on heritable dental characters and do not consider non-heritable variation such as functional disorders (malocclusion and overgrown teeth), variations in the tooth wear patterns, intravital tooth damage, and oral diseases. Sex-related variation in dental characters is considered negligible according to the previous results ([Markova et al., 2010, 2016; 2018, 2019](#)).

To identify age, we consider dental age classes for the sake of compatibility among paleontological and neontological datasets. Most of the species considered in the study possess evergrowing teeth, for which only juvenile and senile age classes might be identified when the materials are represented by isolated teeth. For species with evergrowing teeth, all the discussed patterns are relevant for post-juvenile ontogenetic stages (teeth with juvenile folding of the enamel are not included in the dataset). Laboratory-

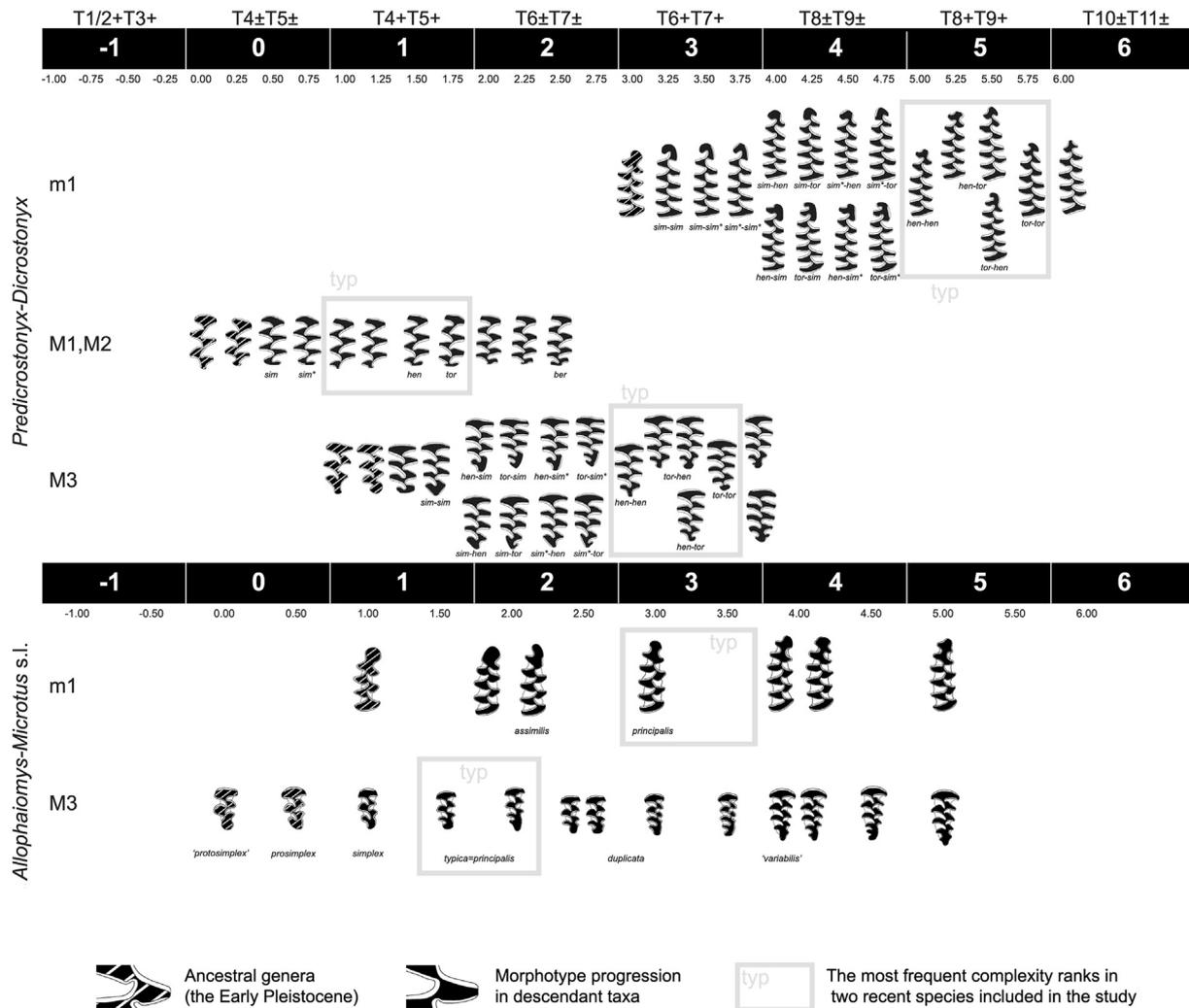


Fig. 1. Correspondence of dental complexity ranks (black bars) to the morphotypes utilised in the practice of arvicoline-based Quaternary biochronology (italics, after Rörig, Börner, 1905; Rabeder, 1986; Smirnov et al., 1986), as exemplified by lineages *Predicrostonyx-Dicrostonyx* and *Allophaiomys-Microtus* sensu lato. The ranks shown in bars are common for all Arvicolinae being based on the presence/absence of fully formed dental prisms T1-Tn (sensu Van Der Meulen, 1973); digits below the bars indicate lineage-specific partitioning of complexity ranks (see Markova, 2014; Markova and Smirnov, 2018 for details). Quotation marks set off the morphotypes, which have been interpreted differently since the first description; asterisks indicate differences within morphotypes related to the presence of enamel; square frames (typ) indicate modal classes of the frequency distributions of complexity ranks in extant terminal taxa considered in this study, *D. torquatus* and *M. arvalis* s.l., including *M. (a.) arvalis* and *M. (a.) obscurus*.

bred animals are primarily three-month old, with few senile individuals used for reproduction. Senile animals were excluded from quantitative comparisons because of the absence of comparable age classes in the datasets from the wild. In samples of *O. zibethicus*, ontogenetic stages were estimated for each molar based on the crown-root ratio (Smirnov, 1960).

Within-individual variation appears to be a significant source of variation in arvicoline dentition because left and right molars of the same category might differ significantly, and the mesial and distal parts of a tooth row appear to be less developmentally stable than the middle parts. Knowing that micromammal assemblages are primarily represented by isolated teeth, we pool left and right molars of the same category in all datasets. To account for developmental modularity of the tooth row, we analyse all molars in all samples and compare the estimates obtained on particular molars (complexity ranks, number of ACS on m1) with those obtained for entire dentition (ACD, average number of ACS).

When considering variation in time, we use geological time scale (Cohen et al., 2016) to assess dental variation within lineages, historical time scale (in years) to address variation in natural

populations of extant species, and the scale of generations when dealing with colonies.

Statistical analysis relied on programs included in STATISTICA 8.0 package (StatSoft, 2007). Tree building was performed in the Fitch module of PHYLIP 3.695 package (Felsenstein, 2004).

2.4. Abbreviations

Abbreviations for all samples and datasets are shown in Supplementary Table A. Laboratory colonies: CK – Kharp, CT – Tiksi, CD – Dvurechensk, F0– founders, F1–F12 – generations of breeding, w – natural source population.

Designation of morphological characters follows the existing nomenclature of arvicoline dentition (Van Der Meulen, 1973) and our previous publications on Lemmini (Markova et al., 2018), *Dicrostonyx* (Markova and Smirnov, 2018), *Microtus* (Markova et al., 2019). Molar teeth (according to their position in tooth rows): M1–M3, m1–m3. Arvicoline dental terminology: ACD – average complexity of dentition, ACS – number of anteroconid separations, AL – anterior lobe, B – buccal, L – lingual, M3_8 – M3 with

additional minor folds in the distal reentrant angles of PL, $M3_{T4T5} \leq 0.5$ – M3 with separated prisms T3 –T4, PL – posterior lobe, RA – reentrant angle, SA – salient angle, T1–Tn – occlusal triangles and respective prisms, typ – modal class of the frequency distributions of complexity and regularity characters. Cricetid dental terminology, upper teeth: AF – anteroflexus, AMF – anteromedian flexus, AML – anteromesoloph, ML – mesoloph; lower teeth: hd – hypoconid, hld – hypoconulid, lpld – labial posterolophid, lpsd – labial posterosinusid (Reig, 1977; Maridet and Ni, 2013). Designations of traits observed on particular molars are indicated by “_”, e.g. m1_lpsd, M1_AMF, etc.

Institutional abbreviations: IPAE – Institute of Plant and Animal Ecology UrB RAS (Ekaterinburg, Russia), PISNR – Pehora-Ilych State Nature Reserve (Komi Republic, Russia).

3. Results

3.1. Laboratory colonies vs. living and extinct populations

3.1.1. Fitness-related traits: crown complexity and occlusal regularity

The degrees of difference between Early Pleistocene and recent members of *Allophaiomys-Microtus* and *Predicrostonyx-Dicrostonyx* lineages are shown in Fig. 2. The grouping of natural and laboratory samples based on the frequencies of m1 and M3 complexity ranks in recent taxa, *M. (a.) obscurus* and *D. torquatus* (Fig. 2, I, III) reveals no geographic structuring and suggests the presence of two principal clusters in both species. Cluster 1 includes all samples with stabilised expression of complexity (typical patterns of m1 and M3 coincide with each other and with species-specific modal classes). Cluster 2 reflects the increased difference between modal ranks of m1 and M3 at the expense of shifts in complexity of M3 towards more complex (*Microtus*) or simple (*Dicrostonyx*) patterns. The differences between clusters 1 and 2 are comparable with those observed among generations in CK, CT, and CD (Appendix B).

Each colony reproduces the entire range of species-specific variability in crown complexity. However, the shape of complexity distributions in CK and CT differ significantly between

the laboratory-bred animals and natural conspecifics tending to become flattened after artificial bottlenecks (Appendix B). Based on the results of clustering (Fig. 2, I, III), the impact of close breeding on dental complexity appears to be the most severe in CT due to the founder effect.

In the cases of decreased occlusal regularity, the ranges of variability strongly depend on founding populations. Accumulation of rare traits with the decreased number of ACS and significant left-tail shifts are found in CK and CD (Fig. 3, III). In CT, we observe only minor fluctuations in the number of ACS, comparable with the natural source population d9.

Along with the flattening of complexity distributions and accumulation of irregular patterns of m1, two of three colonies (CK, CD) produce simplified outliers looking like reversals to the ancestral forms (e.g., Fig. 3I–II). Such atavistically-appearing malformations occur with no intermediate variants.

3.1.2. Extra elements of the occlusal surface: recapitulation of ancestral cricetid features

Extra elements recapitulating cricetid dental features are present in colonies raised for more than two generations. Both the diversity and manifestation of extra characters increase up to generation F6 and then tend to decrease, thus, providing an indirect evidence of inbreeding depression. A comparison with ancestral forms suggests that the rare characters have not been originated in the laboratory but pre-existed in direct ancestors (Fig. 4, I).

An analysis of enamel microstructures in the extra elements of occlusal surface reveals three different combinations of these pleiomorphic characters with the advanced lamellar enamel (Fig. 5). A full-size prism with typical arvicoline pattern of enamel differentiation in place of anteromesoloph (= anteroloph sensu Reig, 1977 or Vorderer Quersporn sensu Fahlbusch, 1964) is found in laboratory-bred *M. (a.) obscurus* (Fig. 5.4 and 5.4 a). A prismatic fold with a non-typical pattern of lamellar enamel in place of mesoloph (Fig. 5.6 and 5.6 a) is found in recent *D. torquatus* on M1 (Ust'-Yuribey and CK), and M2 (Routan Island). An additional fully developed reentrant angle m1_BRAO (=m1_lpsd) in *Dicrostonyx* exhibits lamellar enamel on both leading and trailing edges (Fig. 5.7

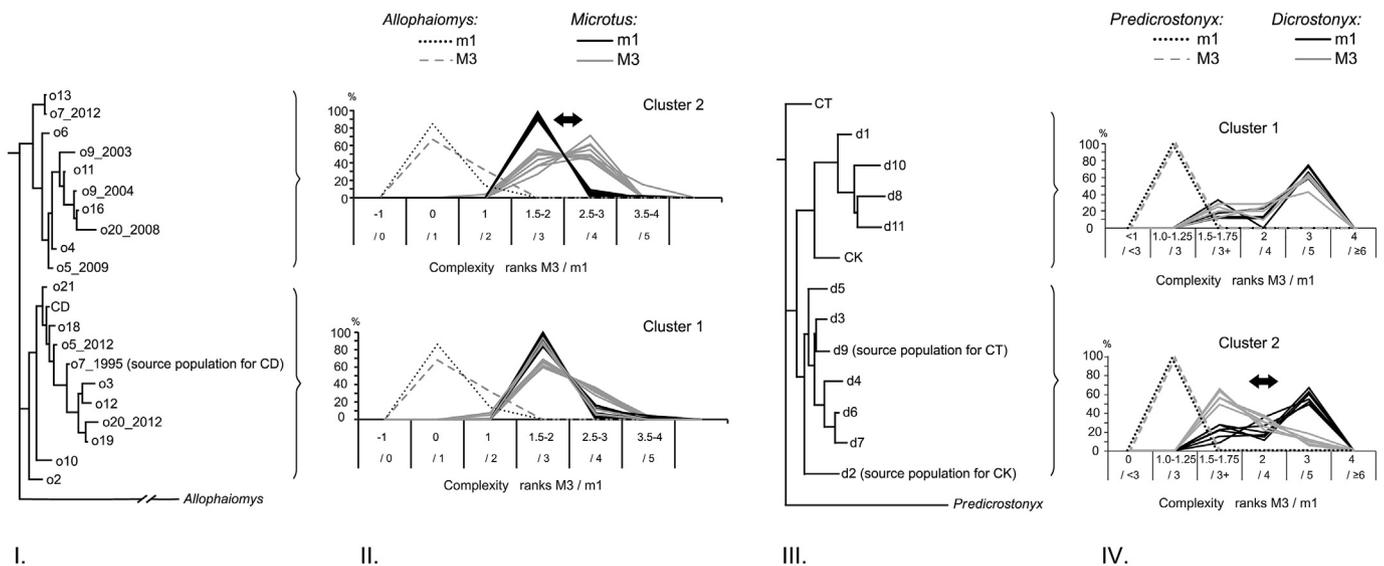


Fig. 2. Crown complexity after artificial bottlenecks in *M. (a.) obscurus* and *D. torquatus*: small number of founders does not reduce the range of variability but affects the shape of the frequency distributions of complexity ranks. I, III – Fitch-Margoliash unrooted trees obtained from dissimilarity matrices based on m1 and M3 complexity ranks in the samples from natural populations and laboratory colonies with the ancestral genera *Allophaiomys* (=A. cf. *A. deucalion*, recalculated from Tesakov, 2004) and *Predicrostonyx* (= *P. ? meridionalis*, samples †d20, †d21) used as the outgroups (see Supplementary Table A for sample details); II, IV – morphological interpretation of the clusters reflecting random fluctuations in dental complexity in time and space; black two-sided arrows – differences between the modal classes of m1 and M3 complexity.

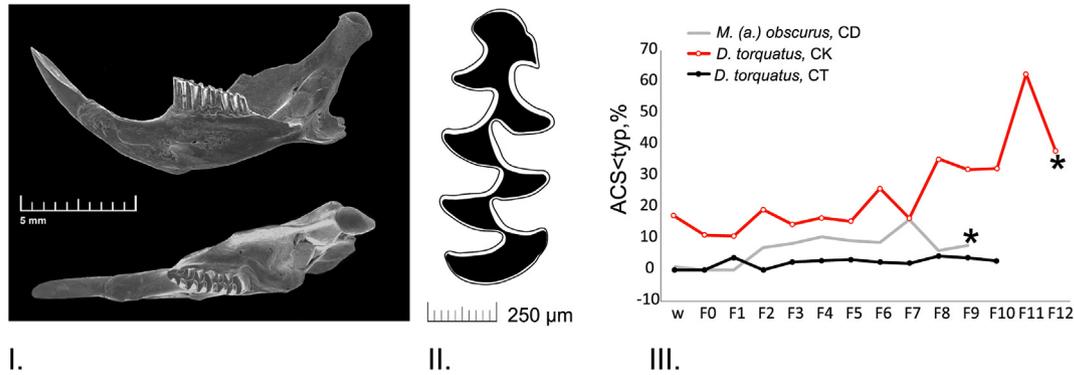


Fig. 3. A case of phenotypic reversal to the ancestral pattern of m1 complexity (*Allophaiomys*-like m1) associated with the loss of m3 in colony CD of *M. (a.) obscurus* (I-II) and accumulation of rare m1 traits with irregular arrangement of enamel cutting edges in the anteroconid complex in colonies CK, CT, CD (III). I – Lingual and occlusal views of the right mandible, II – occlusal outline of m1 of *M. (a.) obscurus* (male C8775, F9, colony CD). III – Frequency of m1 with the decreased number of ACS on m1 in three colonies; asterisks indicate the first occurrence of individuals with reduced anteroconid of m1.

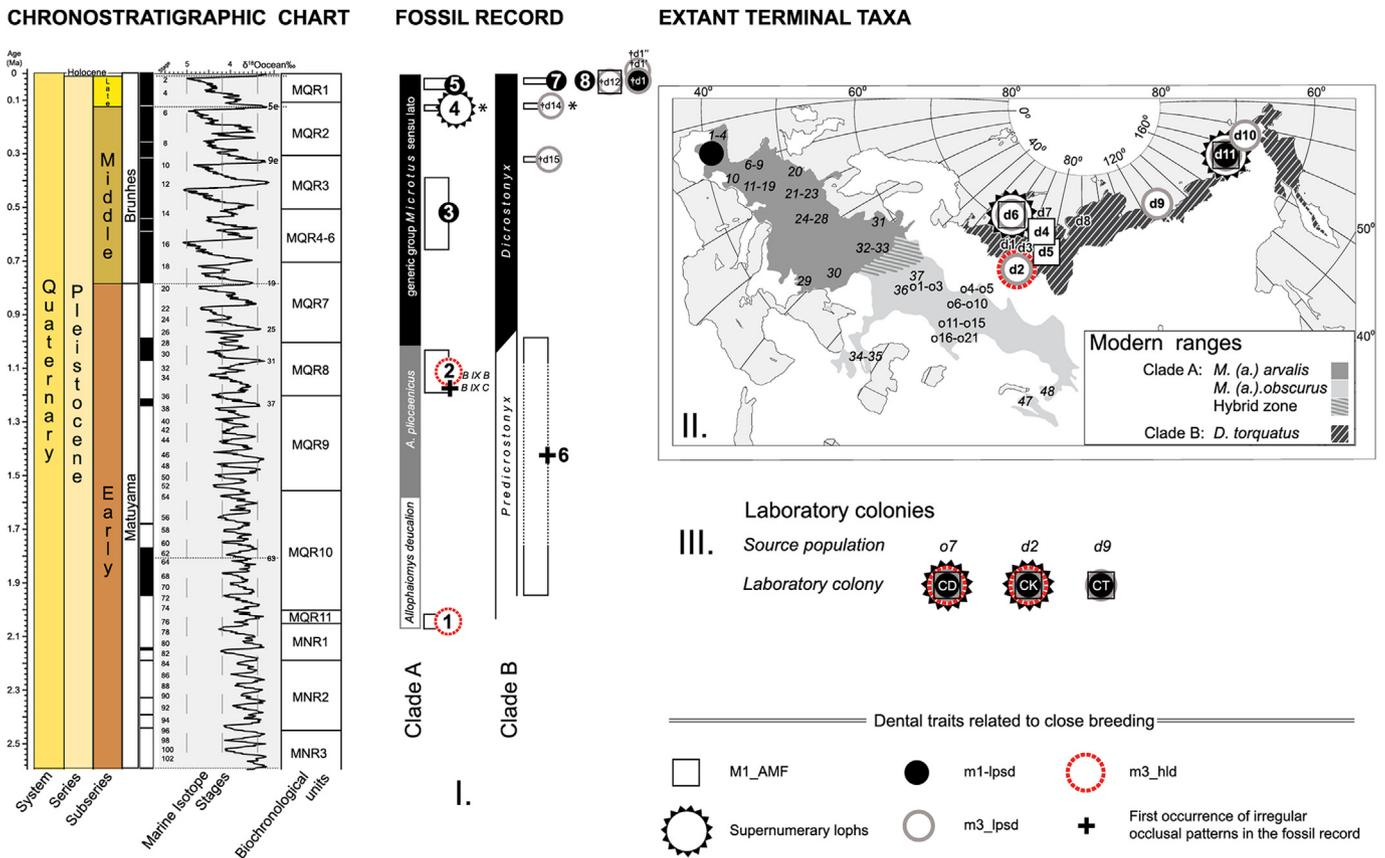


Fig. 4. Occurrence of dental characters related to close breeding in living and extinct arvicolines, as exemplified by *Allophaiomys* – *Microtus* sensu lato (clade A) and *Predicrostonyx* – *Dicrostonyx* (clade B). I – Fossil record of the clades A and B correlated to the International Chronostratigraphic Chart (Cohen et al., 2016) and to the arvicoline-based biochronological units (Krijgsman et al., 2019) showing the localities (1–8, \uparrow d1, \uparrow d12, \uparrow d14– \uparrow d15), time intervals (frames), and synchronous occurrence of dental traits related to close breeding in different taxa in one assemblage (asterisks). 1 – *A. cf. A. deucalion*, Kryzhanovka 4, the Black Sea coastline, Ukraine (Tesakov, 2004); 2 – *A. cf. A. pliocaenicus*, Betfia IX B and IX C, Țașadului Hills, Romania (Hir and Venczel, 1998); 3 – *Microtus meadensis* Hibbard, 1944, Beckman Wash, Borrego Badlands, California, US (Murray et al., 2011); 4 – *Microtus* sp. Yarsino, the upland of Tobolsky Materik, West Siberian Plain, Russia (Smirnov et al., 1986, Fig. 42, 4 therein); 5 – *M. (a.) arvalis*, Arbrede Cave, the Catalan Transversal Range, Spain (Luzi and López-García, 2019); 6 – *Predicrostonyx hopkinsi* Guthrie and Matthews (1971), normally magnetised deposits of the Cape Deceit Formation, the coastline along the Kotzebue Sound, Alaska, the US (Guthrie and Matthews, 1971); 7 – *D. torquatus*, Coulet des Roches, the Vaucluse Mountains (Crégut-Bonnaure et al., 2018); 8 – *D. guillemi*, Koziarnia Cave, layer 2, the Kraków-Częstochowa Upland, Poland (Nadachowski, 1982); \uparrow d1, \uparrow d12, \uparrow d14– \uparrow d15 – this study, see Supplementary Table A. II – Extremely rare manifestation of dental traits related to close breeding in extant cryptic taxa *M. (a.) arvalis* and *M. (a.) obscurus* and increased number of those rare traits in extant populations of *D. torquatus* (1–37, 47, 48 – samples from Markova et al., 2010; o1–o21, d1–d11 – this study, see Supplementary Table A); black circle – recent *M. (a.) arvalis*, Bocigas, Spain (Markova et al., 2010). III – Multiple incidences of the occlusal extra elements in laboratory colonies CD, CK, CT.

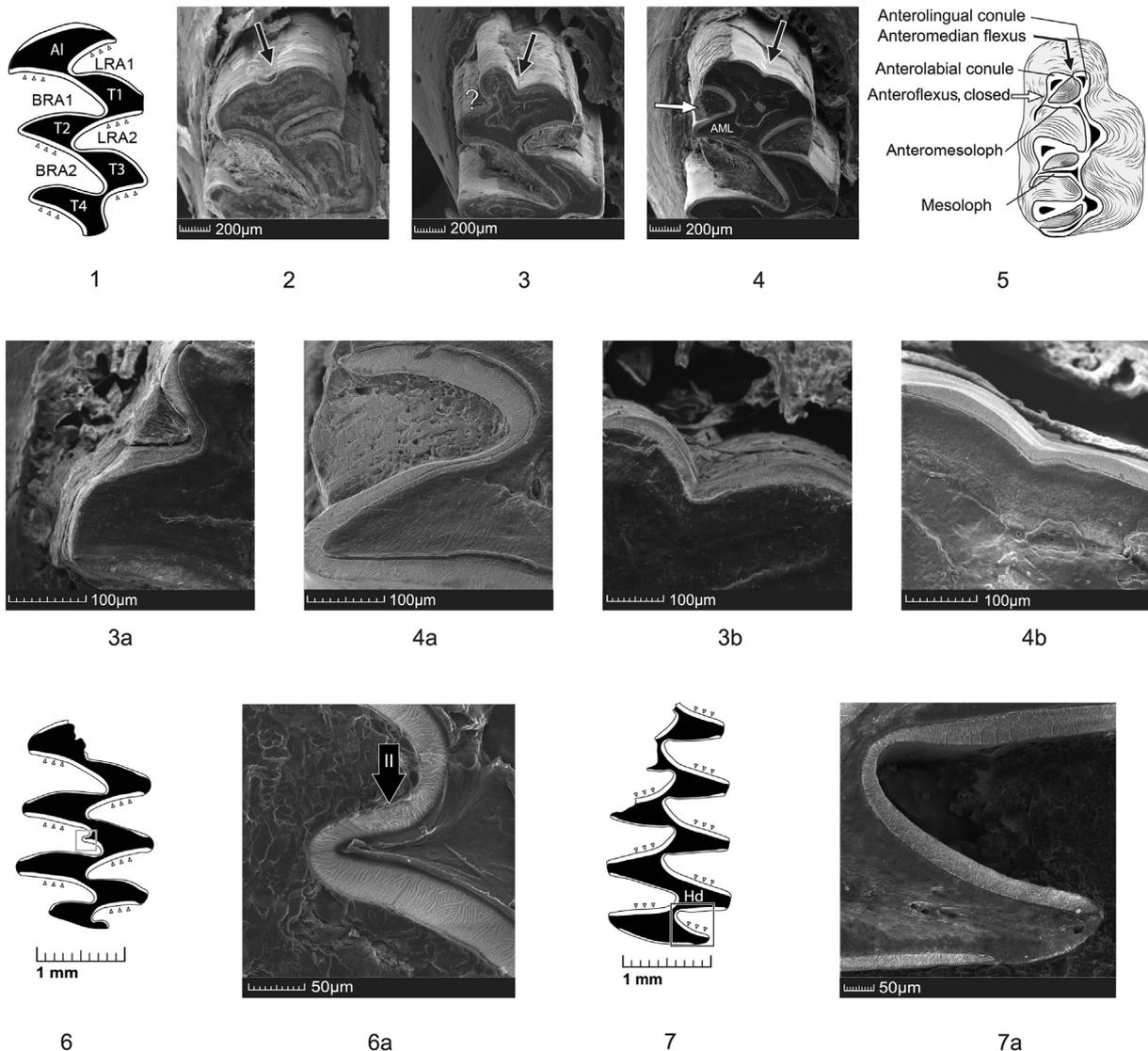


Fig. 5. Plesiomorphic dental characters appearing together with the advanced lamellar enamel in laboratory-bred *M. (a.) obscurus* (1–4), recent *D. torquatus* (6), and extinct *D. guillemi* (7). 1 – A typical M1 of *Microtus* with completely fused elements of AL; 2 – female C6165, colony founder, right M1, mirrored; 3 – female C7293, F4, left M1, mirrored; 4 – female C8231, F6, right M1; 5 – a scheme of M1 of a Miocene cricetid (after [Fahlbusch, 1964](#); modified); a-b – enamel microstructures in the supernumerary reentrant angles BRA0 and LRA0, respectively; 6 – an outline of M1 (left, mirrored) of recent *D. torquatus* from locality d6 (recent) showing a prismatic fold in place of mesoloph (square frame); 6a – enamel microstructure of the prismatic fold in place of mesoloph; 7 – an outline of m1 (right) of *D. guillemi* from locality †d1 (13–21 ka) showing additional T0 formed of hd separated from lpld by lpsd (square frame). Black arrow line – anteromedian flexus, white arrow line – anteroflexus, question mark – second anterior fold on AL that might result from either subdivision of AL by a crest or from an extra cusplet in AMF (e.g., anteromedian style); small open triangles – position of leading edges consisting of lamellar enamel in accordance with the functional requirements; Thick black arrows: I – lamellar enamel in BRA0 appearing on a leading edge in agreement with functional requirements; II – non-typical lamellar enamel in place of mesoloph; III – contradiction between functional requirements and position of the advanced lamellar enamel on the trailing edge of hd.

and 5.7 a). Incomplete or incipient BRA0 on m1 and m3 is found as an infrequent trait in laboratory-bred *M. (a.) obscurus* (up to 0.7% and 0.3%). In all cases, BRA0 homologized with lpsd exhibits typical lamellar enamel (e.g., [Appendix C](#)), which might serve as a criterion to distinguish lpsd from an extra element in place of hld and senile folds on the distal enamel wall (the latter structures exhibit no lamellar enamel).

3.1.3. The dynamics of rare dental traits

An analysis of trait dynamics in isolated artificial populations suggests that any undersampled dental trait (present in the natural source population but not observed among founders) is expected to be phenotypically expressed throughout 9–12 generations of breeding ([Fig. 6](#)). In contrast to complexity and regularity patterns, oversampling of a rare extra trait pre-accumulated in the natural

source population does not lead to significant accumulation of this trait but to recurrence, and rarely to overmanifestation ([Fig. 6, III](#)).

A comparison of laboratory colonies with wild conspecifics suggests that dental aberrations typical for small and inbred populations ([Fig. 4, III](#)) are also present in the wild ([Fig. 4, II](#)), thus not being completely eradicated by large-scale population dynamics. In extant collared lemmings ([Fig. 4, II](#)), rare dental traits recapitulating cricetid features tend to manifest themselves in coastal zones (localities d5, d6, d9, d10), on islands (d11), in declining peripheral populations (d2). In *M. (a.) arvalis*, a single case of such recapitulation has been observed in the southwestern part of the species range ([Fig. 4, II](#)). In *M. (a.) obscurus*, the frequencies of the extra elements of occlusal surface tend to zero in natural populations, although the number of ACS remains a variable trait tending to exhibit higher frequencies of occlusal irregularities (ACS < typ) in

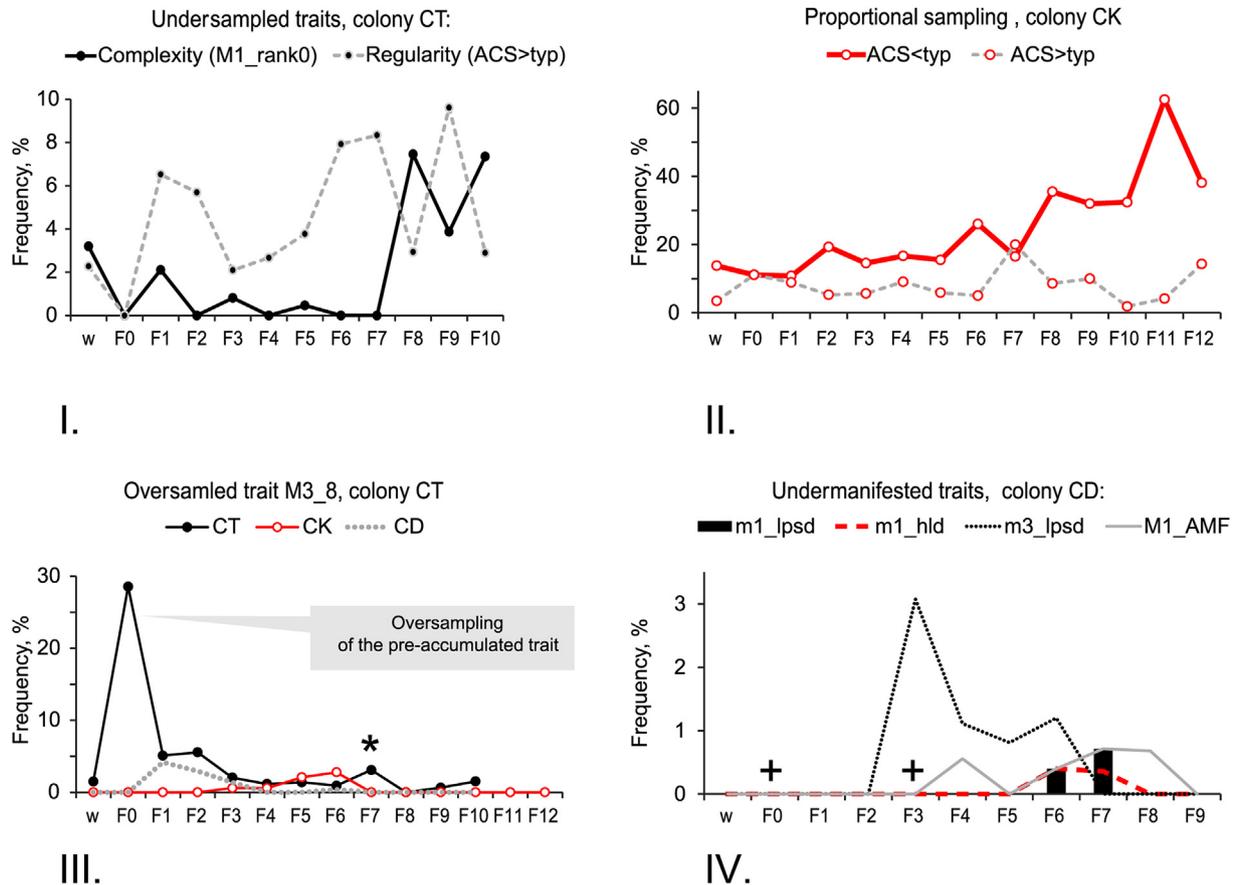


Fig. 6. Trait dynamics in small inbred populations: the effects of an extremely small number of founders (F0) on the frequency of occurrence and manifestation of rare dental traits throughout generations F1–F12 in colonies of *M. (a.) obscurus* (CD) and *D. torquatus* (CK, CT), as compared to the natural source populations (w). Asterisk – overmanifestation of the character M3_8 (subdivided PL into lingual and buccal lobes associated with M3_8 on each lobe), + incipient state of M1_AMF.

local populations during the periods of relatively low species abundance (Fig. 7, II d). The presence of occlusal irregularities (ACS < typ) might also be observed in recent *M. (a.) arvalis* (up to 2%, data not shown) and *M. rossiaemeridionalis* (Fig. 7, III g, IV j). A comparison with the ancestral genera suggests that dental aberrations with occlusal irregularities have been manifested repeatedly over the course of the history of both clades A and B (Fig. 4, I).

3.2. Translocated populations of invasive species

In three of five disjunctive populations of *M. rossiaemeridionalis* occasionally introduced far outside the core range, we observe at least one of the phenotypic shifts suggesting the increased levels of close breeding (Markova et al., 2019). In *O. zibethicus*, we do not observe any phenotypic shift. The pattern of variation in dental complexity is quite conservative (Fig. 8) showing no differentiation between the localities situated in the areas of initial introduction and subsequent expansion (Fig. 8, localities 1–2 and 3–4 respectively). When assessed in complexity ranks, the amount of ontogenetic variation encompasses the range comparable with the range of variation in both the ancestral and descendant genera in the lineage *Allophaiomys-Microtus* (Fig. 2, II). The two age classes established for *Ondatra* by the roots/crown ratio (Smirnov, 1960) represent the two highly differentiated groups in the late summer-autumn samples but the differences tend to diminish during winter. This seasonal pattern of ontogenetic variation in dental complexity is nearly identical in the areas of initial introduction and

subsequent expansion suggesting that the species-specific pattern of variation in fitness-related traits has not been affected by the artificial bottleneck of 247 individuals. Neither aberrant phenotypes nor extra elements recapitulating the cricetid dental features are found in the studied samples.

Thus, the phenotypic shifts are not an inherent characteristic of the invasive populations associated with the artificial bottlenecks. They occur when only a population is spatially restricted inhabiting an island, an oceanic shore, or a city area in the riverine mosaic landscape (respectively, *M. rossiaemeridionalis* on Svalbard, in Sovetskaya Gavan', and Surgut City (Markova et al., 2019)). In the rest of the dataset on the invasive populations, we do not observe phenotypic shifts (*M. rossiaemeridionalis* in the Irkutsk Region, Khabarovsk City (Markova et al., 2019), and *O. zibethicus* in Sverdlovsk Region (this study).

3.3. Island populations

The data on island populations of *Microtus*, *Lemmus*, and *Dicrostonyx* are shown in Fig. 7, b, g–j. In *Lemmus*, the differences between island and continental populations are statistically significant in both complexity ($F_{1;571} = 6.69$, $p = 0.010$) and regularity of M3 ($F_{1;575} = 51.1$, $p < 0.001$), although the only significant and easily observable differences between the island and mainland conspecifics are detected in the datasets from the islands with a distance to mainland greater than 100 km (the New Siberian and Wrangel Islands). In *D. torquatus*, the dataset includes no distant

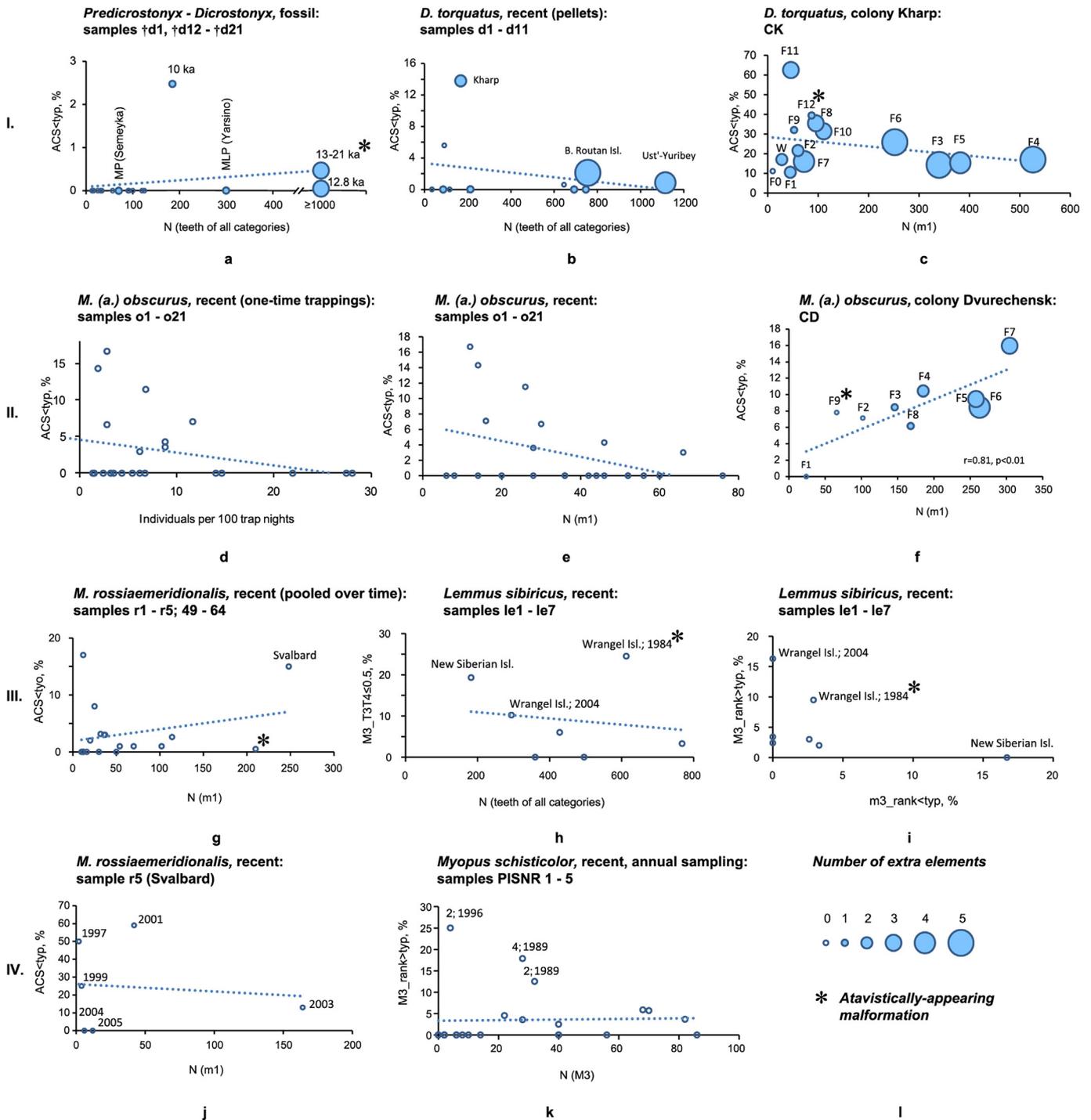


Fig. 7. Frequencies of occurrence (in %) and detectability of rare dental traits in various types of samples: I – *Predicrostonyx-Dicrostonyx* lineage (a - samples from the Early Pleistocene – Holocene localities, the Urals and West Siberian Plain, b – extant populations (birds of prey pellets), c – colony CK of *D. torquatus* raised for 12 generations to study variation in the number of B chromosomes. II - Extant *M. (a.) obscurus* (d-e – wild-living populations studied by one-time trappings, f - colony CD raised to increase the number of homozygous carriers of the acrocentric chromosome 5. III – Island populations compared to the mainland conspecifics (g – *M. rossiaemeridionalis* in the mainland populations and on the Archipelago of Svalbard, h, i – *L. sibiricus* in the island and mainland populations (only the island populations showing significant differences from the mainland conspecifics are indicated), j - *M. rossiaemeridionalis* in a spatially restricted population on the High Arctic Archipelago of Svalbard, k – wood lemming population in the Northern Fore-Urals showing periodic advances and retreats in the heterogeneous landscape, l – legend. Designations: r – Pearson's correlation coefficient, where significant; asterisks indicate atavistically-appearing malformations of m1 (anteroconid loss in *D. torquatus* and *M. (a.) obscurus* and simplified M3 in *M. rossiaemeridionalis* and *L. sibiricus*); circles indicate total number of extra elements of the occlusal surface. See [Supplementary Table A](#) for sample details.

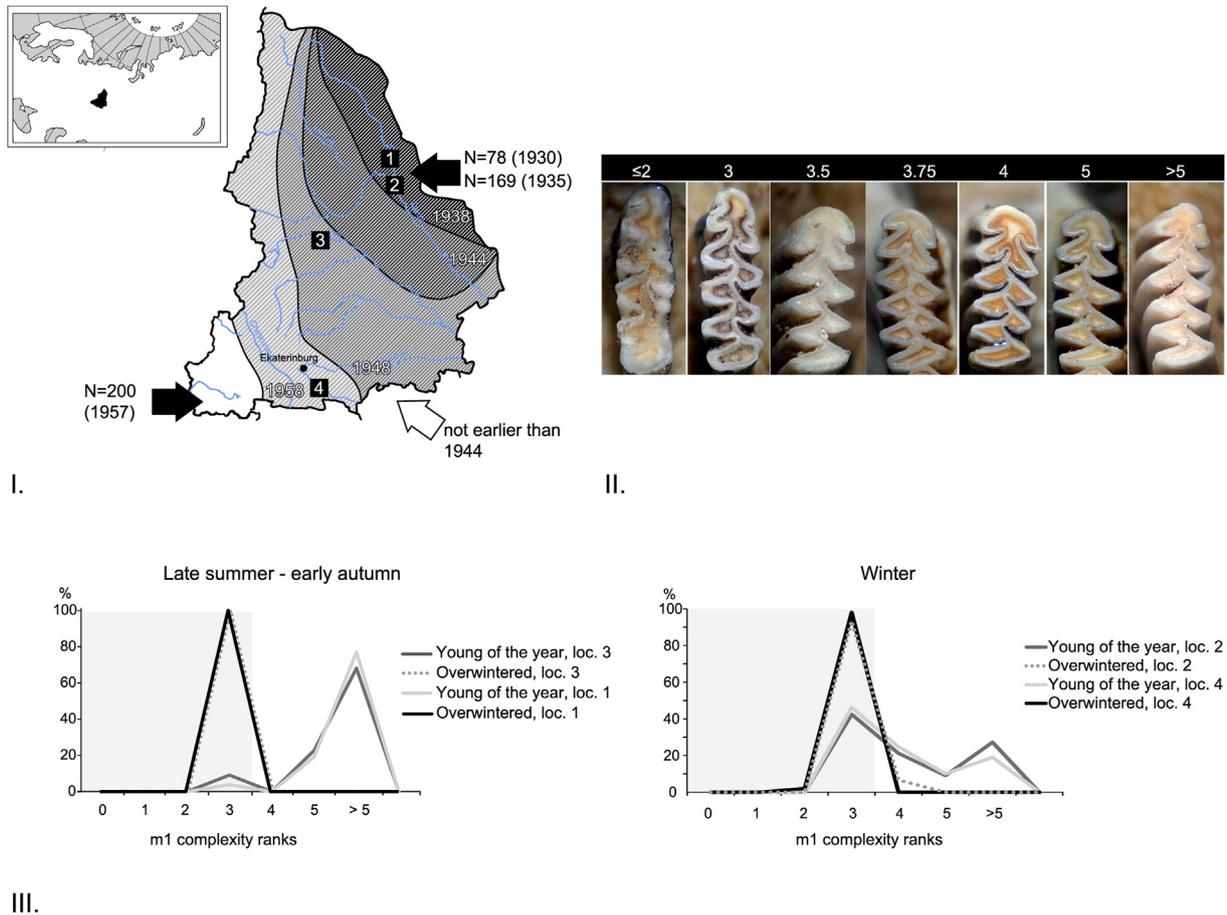


Fig. 8. Expansion in a continuous environment favors phenotypic uniformity: conservative patterns of phenotypic variation in fitness-related characters revealed in *O. zibethicus* expanding to form a continuous range in three-four decades after an artificial bottleneck of 247 individuals. I – A map of Sverdlovsk Administrative Region showing the stages of muskrat introduction (black arrows), subsequent dispersal (dashed gray areas), and the earliest possible contact with the animals from another introduction site (open arrow); 1–4 – sampling localities according to [Supplementary Table A](#). II – Complexity ranks of the first lower molar. III – Frequency distributions of m1 complexity ranks in the samples 1–4 subdivided into age classes based on the crown-root ratio and shown on the background of the range of m1 complexity in an extinct form, *Pliopotamys* (= *Ondatra*) *meadensis* Hibbard, 1938 (gray area).

islands and the most significant differences are observed between the southern peripheral population Kharp, B. Routan Island, and Ust'-Yuribey (Fig. 7, b).

3.4. Population cycles in expanding species

The two model species, *M. schisticolor* and *M. (a.) obscurus* differ significantly with respect to the patterns of landscape use and population dynamics, however the two species exhibit similar pattern of variation in species-specific rare dental traits tending to exhibit higher frequencies in smaller samples (Fig. 7, d-e, k). Repeated sampling in the same localities during different years suggest that the frequency of those traits fluctuates between zero and 17% in *M. (a.) obscurus* and between zero and 25% in *M. schisticolor*. In the island population of *M. rossiaemeridionalis* fluctuations in the frequencies of the same rare trait as in *M. (a.) obscurus* are more pronounced ranging from zero to 59% (Fig. 7, j).

To assess the amount of change in phenotype during local species' advances and retreats on the observable time scale we analyse a population of *M. schisticolor* in the Northern Fore-Urals (PISNR). Previously, it has been shown that the foothills of the Ural Mountains may be considered as the source area for species' dispersal to the lowlands, and the largest species' advances during

the last 30 years have been recorded in 1988 and 2005 (Bobretsov and Lukyanova, 2017). Analysis of the dataset collected in 1988–2010 (Fig. 9) reveals no significant differences in dental complexity between the animals occurring in the source and sink areas ($F_{1,722} = 0.07$, $p = 0.791$), and no difference between the yearly obtained samples ($F_{6,595} = 0.87$, $p = 0.519$). However, two-way ANOVA on the dataset obtained during the outbreaks suggests the existence of significant differences in M3 complexity in time (i.e., between the two outbreaks ($F_{1,453} = 7.6$, $p = 0.006$)), but not in space (i.e., between the source and sink areas ($F_{1,453} = 2.5$, $p = 0.113$)). Spatiotemporal changes might also be traced back by the fluctuations in the frequency of the traits from the right-tail of complexity distribution, or $M3_rank > typ$ (=traits $M3_g$ and $M3_n$ sensu Markova et al., 2018).

3.5. Declining species

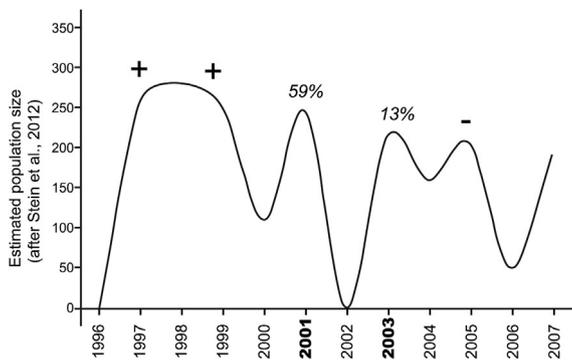
The phenotypic changes in crown complexity and occlusal regularity from the Early Pleistocene *Predicrostonyx* to extant *D. torquatus* and the location maps of the samples included in this case study are shown in Fig. 8. The gradual increase in dental complexity and a saltational change in occlusal regularity characterise the transition from the Early Pleistocene *Predicrostonyx* to the

I. SPATIALLY RESTRICTED ECOSYSTEM

Microtus rossiaemeridionalis, recent:

sample r5 (Svalbard)

m1_ACS<typ

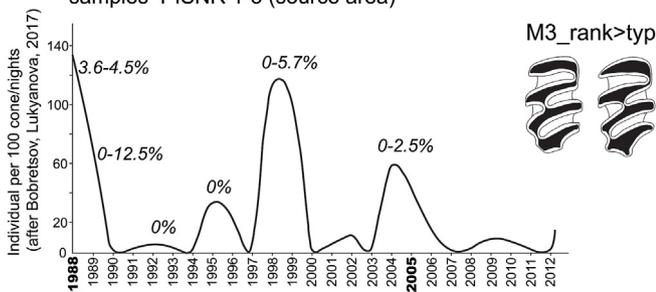


II. SPATIALLY STRUCTURED LANDSCAPE

Myopus schisticolor, recent:

samples PISNR 1-3 (source area)

M3_rank>typ



samples PISNR 4-5 (sink area)

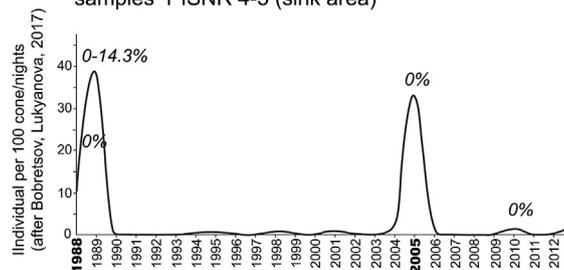


Fig. 9. Statistically significant differences (years in bold, $p < 0.01$) between the datasets obtained during different phases of population cycles: sibling vole in a spatially restricted population on the High Arctic Archipelago of Svalbard (I) and the wood lemming population in the Northern Fore-Urals showing periodic advances and retreats in heterogeneous landscapes of the Pechora-Ilych State Nature Reserve (II). Estimates of the sibling vole population size on Svalbard are redrawn from [Stien et al. \(2012\)](#), the wood lemming abundance is shown after [Bobretsov and Lukyanova \(2017\)](#).

descendant genus *Dicrostonyx*. It is noticeable that the genetic bottleneck at the Late-Pleistocene – Holocene transition ([Prost et al., 2013](#)) is associated with a slight decrease in the average values of both complexity and regularity characters. The two artificial bottlenecks suggest that these changes are comparable to the amount of change between the founders and their offspring in CT (ACD in founders – 11.5, in offspring – 11.45–11.13). However, the

example of colony CK suggests that the offspring of a group of more ‘complex’ founders is getting even more complex on average throughout generations (CK). The effects of bottlenecks on occlusal regularity appear to be even more severe than on complexity, at least when the irregular occlusal patterns are pre-accumulated in the natural source population.

The incidence of dental characters related to close breeding in the fossil record of collared lemmings ([Fig. 4](#), clade B) suggests that irregular occlusal patterns occurred multiple times within the clade starting from *P. hopkinsi* ([Guthrie and Matthews, 1971, Fig. 5](#) therein). The extra elements of occlusal surface occurred regularly at least since the Late Middle Pleistocene.

3.6. Implications for studies of the fossil record

3.6.1. Potential implications for palaeoecological reconstructions

Our results suggest that crown complexity is the most reliable dental character to establish evolutionary trends in *Allophaiomys-Microtus* and *Predicrostonyx-Dicrostonyx* but occlusal regularity is informative when we need to infer local population history and contribution of close breeding to the levels of intra-population phenotypic diversity. It is noticeable that observation of occlusal irregularities in the fossil record of a species at the level of particular locality might predate the occurrence of extra elements of the occlusal surface in the same species and the same locality. Among the examples considered here ([Fig. 4](#), I), we imply *A. cf. A. pliocaenicus* in Betfia IX B and Betfia IX C ([Hir and Venczel, 1998, Fig. 12](#) therein) and *D. gulielmi* in Koziarnia Cave showing ACS < typ in layer 11 and m1_lpsd in layer 2 ([Nadachowski, 1982, Fig. 4](#) therein). Knowing the patterns of manifestation of dental aberrations related to close breeding in extant species, we can potentially hypothesise the existence of local conditions favouring the increased levels of genetic drift in the localities where the phenotypic markers of close breeding occur repeatedly in a sequence of assemblages. When the characters related to close breeding occur simultaneously in different species in one assemblage ([Fig. 4](#), localities marked with asterisks), we can potentially hypothesise the impact of fast progressive changes in the entire community (e.g., ecological successions).

3.6.2. Detection of phenotypic reversals in biochronological index taxa

Laboratory colonies as artificial bottlenecks allow us to assess the extent of phenotypic reversibility in dental characters caused by close breeding. When founder effect results in gradual simplification of dentition, this simplification might result in the accumulation of plesiomorphic morphotypes (e.g., morphotypes sim and hen of M1 in generations F8–F10 in CT). The percentage of these morphotypes during F8–F10 in CT tends to recapitulate the percentage typical for the ancestral chronospecies *D. gulielmi*, morph 3 (sensu [Smirnov et al., 1997](#) and [Ponomarev and Puzachenko, 2015](#)). In M2, this simplification appears to be less pronounced keeping the percentage of morphotypes within the range typical for *D. torquatus*, morph 2 in all generations. The increased differences in complexity among different categories of molars in one sample may serve as important indicators of possible phenotypic reversals due to genetic drift (at least in cases when the second molars exhibit more advanced patterns of complexity and simplification occurs mesially and/or distally of m2 and M2). When associated with accumulation of occlusal irregularities and/or multiple incidence of the extra elements of occlusal surface, the cases of increased differences in complexity ranks estimated for different tooth categories should be interpreted as the signs of an isolated, locally declining, or spatially restricted population.

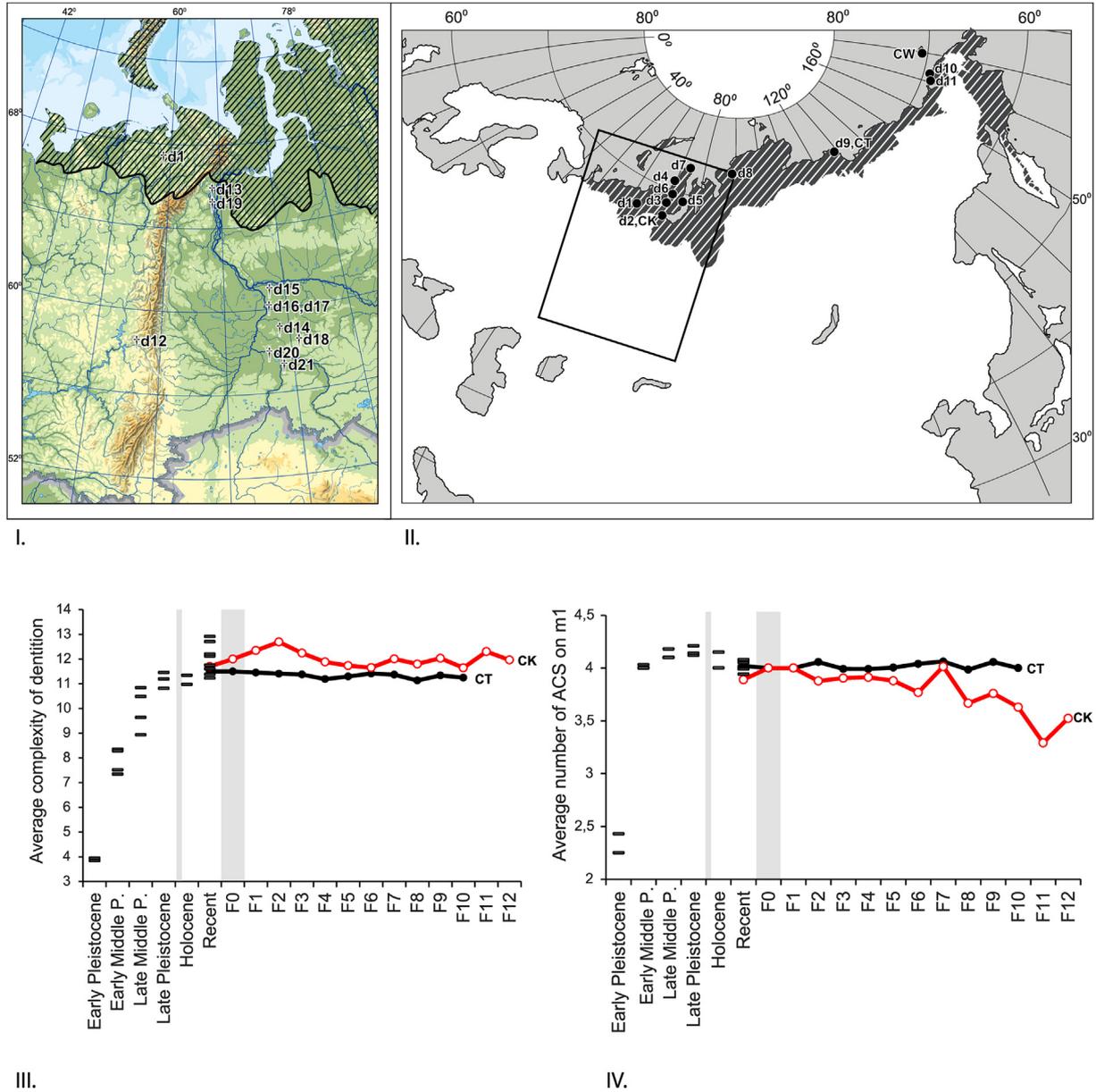


Fig. 10. Collared lemmings surviving natural and artificial bottlenecks, as compared to the ancestral forms dated back to the Early Pleistocene (*P. meridionalis*), early Middle Pleistocene (*D. simplicior*), late Middle Pleistocene (*D. cf. D. henseli*), Late Pleistocene (*D. cf. D. guillemi* and *D. torquatus*), and Holocene (*D. torquatus*). I – II - Location maps of the fossil assemblages (I) and modern samples (II); III – IV – phenotypic changes in the overall complexity of dentition, ACD (III) and occlusal regularity of the lower first molar (IV). Thin gray area – relative temporal position of a natural bottleneck previously detected by molecular-genetic methods (Prost et al., 2013), thick gray area – founding generation F0 of the colonies CK and CT considered as artificial bottlenecks. Black line markers – fossil assemblages and recent natural populations (except for the populations Kharp and Tiksi marked to show the relatedness to the respective colonies CK and CT); black solid line with black dots – colony CT originated in 1973 from a persisting population, red solid line with open dots – colony CK originated in 1971 from a southern peripheral population, recently extinct, P. – Pleistocene. See Supplementary Table A for sample details. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

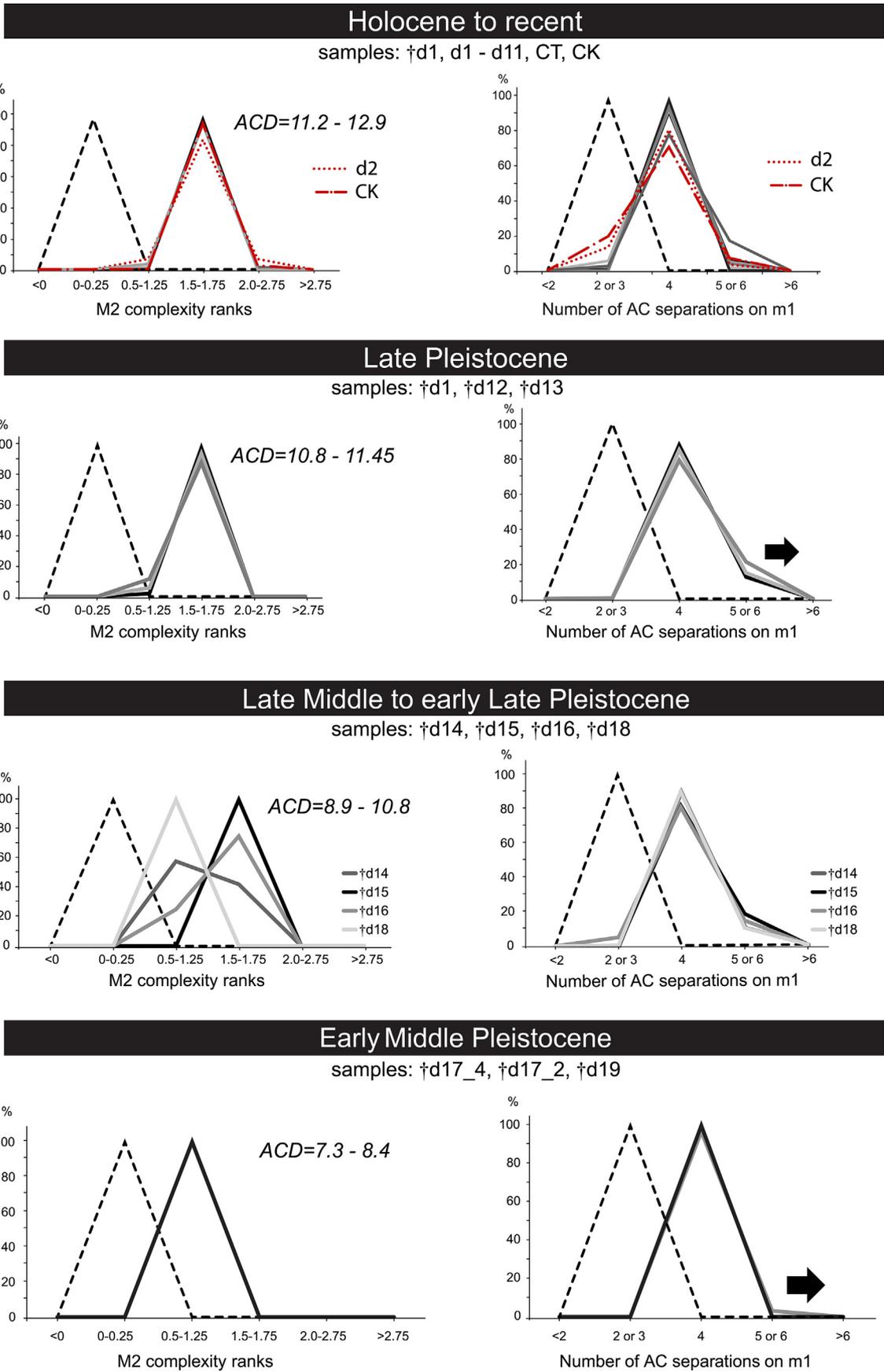


Fig. 11. Morphological changes in dentition of collared lemmings in the central part of Northern Eurasia during the last 1 myr illustrated by the comparison of the previously identified chronospecies *D. simplicior* - *D. cf. D. henseli* - *D. cf. D. gulielmi* - *D. torquatus* (Smirnov et al., 1986; Borodin et al., 1998; Kosintsev et al., 2004) with the ancestral form, *P? meridionalis*. Complexity of dentition is characterised by the complexity ranks of M2 as the most inbreeding-resistant element of the tooth row; occlusal regularity is characterised by the number of anteroconid separations on m1; dashed black line indicates *P? meridionalis* from localities †d20-21; dotted red lines indicate a peripheral population of *D. torquatus* (locality d2) extinct since 1970s (see Supplementary Table A for sample details). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

3.6.3. Identification of expanding and declining stages within one phyletic lineage

Following the observation that population expansions in extant arvicoline rodents favour phenotypic uniformity and the declines lead to sporadic accumulation of rare traits, and knowing the limits of variation due to genetic drift in the extant terminal taxon of the lineage *Predicrostonyx-Dicrostonyx* (Fig. 10), we can distinguish between expanding and declining stages within one phyletic lineage and to compare these stages with traditional chronospecies (Fig. 11).

The samples characterizing the early Middle Pleistocene are represented by *D. simplicior* Fejfar, 1966 from localities Chembakchino 2, 4, and Khashgort. Average complexity of dentition, ACD = 7.3–8.4.

In the late Middle Pleistocene – beginning of the Late Pleistocene, the samples are represented by *D. cf. D. henseli*, Hinton (1910) from localities Chembakchino 12, Yarsino, Shakhmatovka II, Semeika. Average complexity of dentition, ACD = 8.9–10.8 but the trends revealed for particular teeth are quite different (e.g., the modal classes of M2 complexity are not the same (Fig. 11, †d14–d16, †d18). In localities Yarsino and Semeika, the extra elements recapitulating cricetid dental features are observed for the first time (m3_lpsd and m1_8).

The Late Pleistocene samples (localities 430 km, Pymva-Shor I, layer 6, Dyrovaty Kamen' on the Chusovaya River) have been previously identified as either *D. cf. D. gulielmi* Sanford, 1870, *D. torquatus*, or *Dicrostonyx* sp. Our results show that the samples exhibit the same complexity rank of M2 (Fig. 11), and ACD = 10.8–11.45. Most of the extra elements of the occlusal surface observed in the laboratory colonies of *D. torquatus* are present in the samples from Pymva-Shor I, layer 6 and Dyrovaty Kamen' on the Chusovaya River.

Recent stage of the evolution of collared lemmings after the Late Pleistocene – Holocene transition is represented by *D. torquatus* (ACD = 11.22–12.9). The distributions of both complexity and regularity characters reveal the accumulation of rare traits on both right and left tails, and this tendency is the most clear in the natural peripheral population Kharp, and its laboratory offspring.

Knowing that population declines and population bottlenecks in recent lemmings are characterised by accumulation of rare traits on both sides of the character distributions, we can detect similar patterns of rare traits accumulation in the samples dated back to the late Middle Pleistocene and the beginning of the Late Pleistocene. In the samples dated back to the early Middle and Late Pleistocene (after Marine Isotope Stage 5e), we observe one-tailed distributions of dental complexity accompanied by the one-tailed distributions of occlusal regularity. This, along with the lack of rare traits, might be a characteristic of an expanding stage favouring phenotypic uniformity and directional evolutionary trends forced by natural selection.

4. Discussion

Our results on the colonies of *Dicrostonyx* and *Microtus* suggest that an artificial bottleneck event consists of three periods. First is the reproduction of the species-specific range of variability in fitness-related traits, here – complexity ranks (generations F1–F2). In arvicoline rodents, 6–10 founders is enough to reproduce the species-specific range of variability in crown complexity, and 21 founders might perfectly reproduce both the range and shape of the distribution of complexity ranks. Second stage is the release of hidden phenotypic diversity caused by the increasing rates of

inbreeding. At this stage, we observe the highest diversity of malformations and atavistic extra elements. Then the diversity of dental aberrations tends to decrease. At the latter stage of recovery, the specimens resembling the ancestral genera might occur as the outliers with no intermediate variants. Although the frequency of atavistic extra elements is getting lower after the inbreeding depression, the manifestation of atavisms does not show a tendency to decrease. Once intensified by inbreeding, the atavistic characters do not play back their expression to an initial state observed prior to the bottleneck. Thus, the frequency of atavisms keeps around single percent or zero but their manifestation increases.

A comparison of the colonies with natural populations suggests that aberrations typical for small and inbred populations are diminished but not eradicated by large scale population dynamics. Being present in natural populations as rare traits, dental characters associated with close breeding might serve as the indirect markers of local population structuring and/or reduction in the number of breeding individuals.

4.1. Which dental characters are the best to detect a bottleneck? A practical perspective

Although phenotypic reversals have been discussed for a long time in evolutionary studies (Gingerich and Schoeninger, 1977; Dercole et al., 2002; Rebolleda-Gómez and Travisano, 2019), this problem has never been thoroughly addressed from a biochronological point of view. Joint analysis of paleontological and neontological datasets allows us to suggest that phenotypic changes induced by severe population bottlenecks might be counter-directional with the selection-driven evolutionary trends in dentition observed in arvicoline lineages during the Quaternary. The reversals are not negligible because the accumulation of simplified patterns owing to the founder effect might bias the range of variation to the level of an ancestral chronospecies (e.g., accumulation of simple M1 morphotypes in CT). Moreover, the occurrence of specimens recapitulating the levels of complexity typical for ancestral genera might compromise diagnostic accuracy and lead to mistakes in species lists. When overlooked, the consequences of severe population bottlenecks may be detrimental for biochronological interpretations of the arvicoline assemblages. Fortunately, the consequences of close breeding in an isolated group are usually multiple and might be figured out as far as the sample is large enough. Our practical observations suggest that minimum number of teeth to recover rare traits in a species in an assemblage from fluvial sediments is about 55 and the probability to recover rare traits increases with the increasing sample sizes. Interestingly, when dealing with extant populations the situation is quite different. The probability of trapping an individual with a rare dental trait is higher during the periods of low species abundance, when the species is confined to source habitats (e.g., *M. (a.) obscurus*) or live in ephemeral local populations formed after major outbreaks (e.g., *M. schisticolor*). This principal difference between fossil assemblages and natural populations is important because all fossil assemblages represent wider spatial and temporal scales than any result of animal trapping.

We suggest that total number of all traits related to the over-expression of non-specific ancestral variation on all molars in all individuals in a neontological sample or summary frequency of all of those traits in paleontological samples may serve as a marker of the increased genetic drift with a noticeable contribution of close breeding in the natural source populations. However, when finding

a marker of close breeding in an assemblage, we can only say that the species existed under the conditions that favoured formation of small isolated groups. We cannot say why and how did it happen, was it a long-lasting population bottleneck or an ephemeral isolation of a family group until we study a series of samples from the same territory from a particular period.

In our case study on *Dicrostonyx*, we first observe the signs of inbreeding-induced variation in the assemblages dated back to the late Middle Pleistocene (Semeika) and from the very beginning of the Late Pleistocene (Yarsino). Dental variation in *Dicrostonyx* cf. *D. henseli* in these localities has been thoroughly studied (Smirnov et al., 1986) and the discrepancies between the geological and biochronological interpretations of the age of the assemblages have been referred to as the result of reworking. However, the occurrence of m3s with lpsd along with the increased frequency of the traits on the tails of the frequency distributions of occlusal regularity allows us to propose another scenario. We hypothesise that the signs of the intensified genetic drift in collared lemmings might be associated with patchy distribution of the species in heterogeneous landscapes. The samples are collected from the deposits of Chembakchino Formation of fluvial origin, rich in *Corbicula* remains (the upper layers of Tobol Horizon, ca MIS 9) and from the above-lying Yalbynya Formation correlated with the beginning of MIS 5. The peculiarity of these assemblages might not be a mere result of taphonomic factors. The presence of non-single specimens exhibiting the traits associated with close breeding and accumulation of rare traits of occlusal regularity in *Dicrostonyx* collectively suggest that lemming populations were subject to genetic drift and the rates of close breeding were higher than in the assemblages of the preceding and succeeding periods. Knowing the patterns of accumulation of rare traits in the terminal taxon of the lineage (extant *D. torquatus*), we can hypothesise that the animals existed under conditions of highly fragmented landscapes favouring genetic drift. In Yarsino, extra elements on the occlusal surface are also quite typical for *Microtus* molars (Smirnov et al., 1986, Page 108, Fig. 42). Although taxonomic interpretation of aberrant *Microtus* in Yarsino demands revision, the similarity of phenotypic patterns in two different genera clearly shows that the entire community was affected by a common environmental factor. The most probable factor that might induce significant fragmentation of the available habitats was the increased sea levels and formation of island-like landscapes.

It is noticeable that in the north of the West Siberian Plain the declining stages of *Dicrostonyx* lineage are identified in the assemblages correlated with the periods of marine transgressions in MIS 9 and MIS 5e. In northeast European Russia, the phenomenon of mosaic evolution in collared lemmings has been suggested for the assemblages correlated with the stage MIS 5e based on the synchronous occurrence of different chronospecies (Ponomarev and Puzachenko, 2015). Our results suggest that formation of multiple spatially restricted populations with the increased levels of close breeding might have acted as the driving force for mosaic phenotypic changes that are not necessarily associated with coexistence of different taxa but might reflect the processes of genetic drift at the intraspecific level.

Thus, the expanding and declining stages within one phyletic lineage might be potentially differentiated by means of morphological criteria applicable to both living populations and fossil assemblages. These morphological criteria deserve further development because the periods of expansions appear to be better represented in the fossil record, while the periods of decline remain poorly understood.

4.2. A developmental perspective

The recurrence of non-specific ancestral traits in dentition of arvicolines surviving bottlenecks in captivity or living in the areas favouring genetic drift, as well as the presence of those extremely rare traits in the ancestral forms of different evolutionary levels collectively suggest the existence of a common morphogenetic mechanism responsible for the release of ancestral variation in Arvicolinae.

When considered in terms of crown complexity and occlusal regularity, all the variety of dental traits in arvicoline dentition might be traced back to the early stages of tooth morphogenesis. Initiation and development of teeth is under control of the genes related to several signaling pathways, WNT, MBP, HH, FGF, and EDA (Thesleff, 2018). Arvicoline-specific patterns of dental complexity, i.e., the number of tooth cusps in an embryo, are related to the expression of *Fgf4*, *Lef1*, *p21*, and *Shh* genes (Jernvall and Thesleff, 2000). Formation of crests appears to be related with the variations in the expression of the *Eda* pathway genes (Kangas et al., 2004; Charles et al., 2009; Rodrigues et al., 2013). When studying dental variation in arvicoline rodents, living and extinct, we find neither multiple additional cusps nor fused teeth typical for the mutants with the disrupted *Shh*-WNT signaling (Seppala et al., 2017; Cho et al., 2011). However, we find the traits typical for mutant mice with over- or underexpressions of the *Eda* pathway genes (Kangas et al., 2004; Rodrigues et al., 2013). In *M. (a.) obscurus*, these characters first appear in generation F3 as a result of inbreeding. In *D. torquatus*, those characters are pre-accumulated in the wild, and close breeding increases the manifestation of those traits.

In laboratory generation F12 in *D. torquatus* and F9 in *M. (a.) obscurus* we observe individuals with major transformation of lower dentition appearing with no obvious transitional forms. Those animals exhibit a simplified m1 (to the level of the ancestral genera) in one mandible, and only minor signs of the underexpressed occlusal regularity in another. Appearance of such morphology might not be explained by an alternation in the *Eda* pathway alone and should probably involve one of the inhibitors or an abrupt rearrangement in the activation/inhibition balance, the genetic background of which is yet to be uncovered (e.g., Navarro and Maga, 2018). The possibility of Arvicolinae to develop ancestral phenotypes by an abrupt backward change in dental complexity with no apparent intermediate states deserve further studies because it might potentially shed light on the developmental mechanisms involved in saltational patterns of speciation observed in this group of rodents during the Quaternary.

4.3. From the tail of a character distribution to a new mean, or to extinction?

Considering dental features as the characters with bell-shaped patterns of expression provides a way to compare ancestral forms directly with their living descendants and to determine directions and amounts of trait change observed on different time scales. The shifts of modal classes in the distributions of fitness-related dental characters (complexity and regularity) are accompanied by the appearance of rare traits on the right and left tails of the frequency distributions. The founder-induced shifts in complexity are non-directional but the rare traits from the tails are always indicative of the modal class typical for the population. Strictly one-sided accumulation of the tail traits suggests the shift of the mean to the same direction but sometimes the rare traits are accumulating

on both left and right tails. In our dataset, two populations exhibit the highest rates of simultaneous accumulation of rare traits on both left and right tails of the distributions of complexity and regularity. The first is the recently extinct peripheral population of *D. torquatus* in Kharp and the second is the island population of *L. sibiricus* on Wrangel Island known to exhibit the significant decrease in genetic diversity (Fedorov, 1999). The significant phenotypic peculiarity of *L. sibiricus* from Wrangel Island has been previously shown by Abramson (1993). Our study suggests that this peculiarity is a consequence of the accumulation of rare traits, which appears to be typical for arvicolines living in isolation. However, the accumulation affects two tails of the frequency distributions (increased frequency of both simplified and complex ranks) and a simplified pattern of M3 with the loss of Lemmini-specific morphology in its distal part is detected (Fig. 7, II-h, i), thus suggesting multiple signs of close breeding and/or a past bottleneck event.

Phenotypic outliers are quite different from the tail traits because they fall outside the species-specific range of variability. Being separated from the species-specific normal range of variation, the outliers appear only on the left tail of the distributions of complexity and regularity. They may look either abnormally developed or like 'hopeful phenotypes' resembling ancestral forms with no obvious signs of the loss of fitness. In contrast to the gradual accumulation of rare traits on the tails of the distributions, the appearance of outliers is a saltational change. Two cases of such saltational alterations are detected and both appear few generations after the period of inbreeding depression in the laboratory colonies (CK, CD). The occurrence of atavistically-appearing 'hopeful phenotypes' might be considered in the context of the old and debatable 'hopeful monster hypothesis' that attracts new attention in recent times (Theißen, 2006) or within the framework of evolutionary models incorporating saltational changes (for arvicolines: Chaline et al., 1993). Our findings in arvicoline rodents provide an evidence that abrupt developmental reversals recapitulating major evolutionary transitions similar to those observed between the ancestral and descendent genera might occur as a result of close breeding.

We suggest that accumulation of rare traits on both sides of the distributions of fitness-related dental traits in arvicolines associated with the increased rates of within-individual variability and the release of hidden ancestral variation provide a cumulative evidence of population decline. The increasing number of such populations within the range provides an evidence of the species decline. When declining to an extreme rate of inbreeding, the most advanced arvicoline species appear to be capable to lose some of their evolutionary achievements and to produce 'hopeful monsters' that might be interpreted as stochastic developmental experiments to maintain the lineage when the species is prone to extinction.

Accumulation of the deviations from the species-specific occlusal regularity and phenotypic expression of the early cricetid traits in arvicoline dentition disrupt species-specific patterns of dental morphology, thus compromising fitness-related dental traits and inducing morphological disparity. The rate of accumulation of such traits in extant *D. torquatus* appears to be unprecedented and deserves particular attention that should be directed towards the evaluation of the extinction risk for this species.

5. Conclusions

In arvicoline rodents, population bottlenecks increase diversity in fitness-related dental characters (crown complexity and occlusal

regularity) owing to the founder effects, and release hidden phenotypic variation owing to inbreeding.

Founder effects lead to non-directional shifts of modal classes in the frequency distributions of dental complexity and occlusal regularity (as observed starting from F1). At the level of particular populations, such shifts might potentially lead to the changes counter-directional with the evolutionary trends inferred from the fossil record of the lineage, to which the species belong.

Inbreeding-induced release of hidden phenotypic variation is observed by the appearance and increased manifestation of non-species-specific extra elements of the occlusal surface in places of the early cricetid tooth structures (transverse lophs and secondary cusplets) and appearance of simplifications resembling ancestral forms. Appearing on the background of the apomorphic characters (hypsodont teeth, advanced enamel types), the extra structures and atavistically-appearing malformations may serve as the markers of close breeding in arvicoline populations. Being present in both living and extinct species, the rare dental traits associated with close breeding appear to be promising to account for possible biochronological discrepancies related to the increased genetic drift in natural populations of the arvicoline proxies and index taxa used in the Quaternary biochronology and biostratigraphy.

Application of the results to the fossil record of collared lemmings from the north of West Siberia allows hypothesising the periods of the increased genetic drift in the ancestral forms of *D. torquatus* in the late Middle Pleistocene and in the early Late Pleistocene.

An example of collared lemmings suggests that extant species might be capable of dental phenotype reversals to the level of the nearest expanding stage in the same lineage. Although the reversibility of traits does not imply the reversibility of phylogenetic stages, the ability of biological species to express phenotypic reversals in small isolated groups of breeding individuals should be taken into account in biochronological studies when interpreting the evolutionary levels and delineating the boundaries of particular chronospecies.

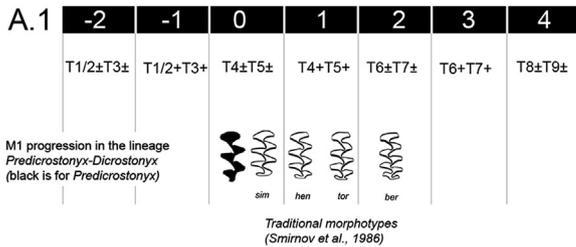
CRediT authorship contribution statement

Evgenia Markova: Conceptualization, Methodology, Investigation, Formal analysis, Validation, Writing - original draft, Project administration. **Anatoliy Bobretsov:** Investigation, Data curation. **Aleksandr Borodin:** Investigation, Supervision. **Sergey Rakitin:** Investigation, Data curation. **Petr Sibiryakov:** Investigation. **Nikolai Smirnov:** Investigation, Supervision. **Lidia Yalkovskaya:** Investigation. **Sergey Zykov:** Investigation, Visualization.

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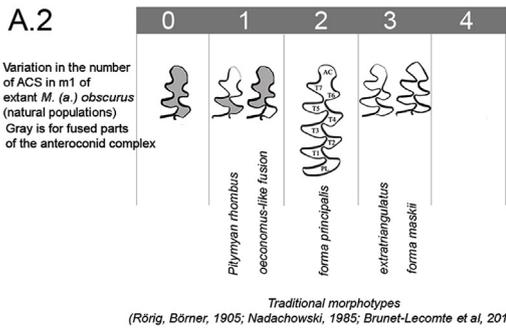
We wish to thank M.R. Bokachev (Ekaterinburg, Russia) for providing the archive data of the Sverdlovsk Society of Hunters and Fishermen collected by R.I. Bokachev, and Prof. V.S. Zazhigin (Moscow, Russia) for providing two samples of birds-of-prey pellets. We are also grateful to the curators of the Museum of the Institute of Plant and Animal Ecology UrB RAS (Ekaterinburg, Russia) for their assistance. The study was performed in the framework of the State Contract with the Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences, and partially supported by Russian Foundation for Basic Research, grants № 16-04-01486 a, 19-04-00966 a.

Appendix



Crown complexity ranks (I)

Complexity ranks (Markova, 2014) - an interval scale defined by the presence/absence of fully formed dental prisms T1-Tn (sensu van der Meulen, 1973) and subdivided into intervals following the underlying developmental mechanism of pairwise cusp formation in an embryo (Jernvall et al., 2000)

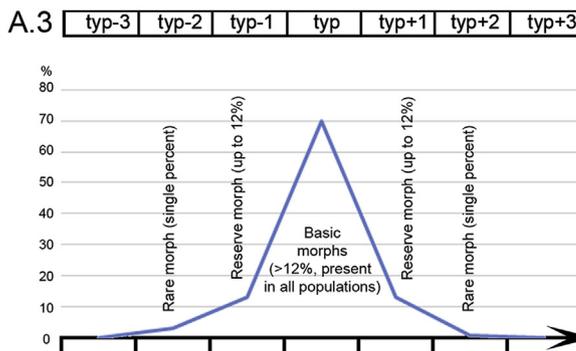
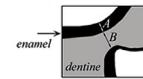


Occlusal regularity indexes (II)

Traditional ordinal scale defined by the number of completely separated prisms in an arvicoline molar considered in this study as the reflection of a single phenotypic pattern tentatively related to the formation of the longitudinal crest (e.g., the number of anteroconid separations, ACS)

Criteria for definition of the extent of fusion/separation between the prisms:

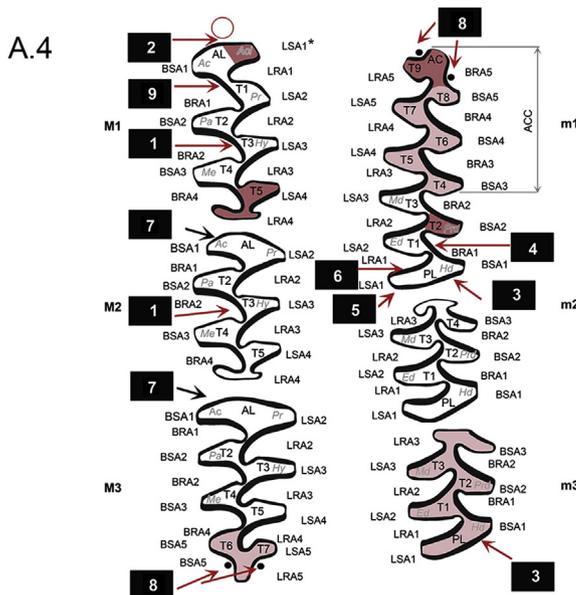
A<B - 1, fusion
A=B - 0.5, incomplete separation
A>B - 0, complete separation



Designation of character states at the level of species used in this study to show positioning of a trait relative to the modal class (typ) of the distribution (an empirically-based model for understanding the range of variability in characters I and II at the level of species)

Terminology for the frequency of dental traits in arvicoline populations, living and extinct (Bolshakov et al., 1980, modified)

The extent of phenotypic expression of dental characters I and II



Extra elements of the occlusal surface

Trait number (after Markova, Smirnov, 2018, modified)	Homology with cricetid features**	Trait designation in this study
1	ML	M1_ML, M2_ML
2	AMF	M1_AMF
3	lpsd	m1_lpsd, m3_lps
4	emld	
5	hld	m3_hld
6	?	
7	?	
8	?	m1_8, M3_8
9	AML	M1_AML

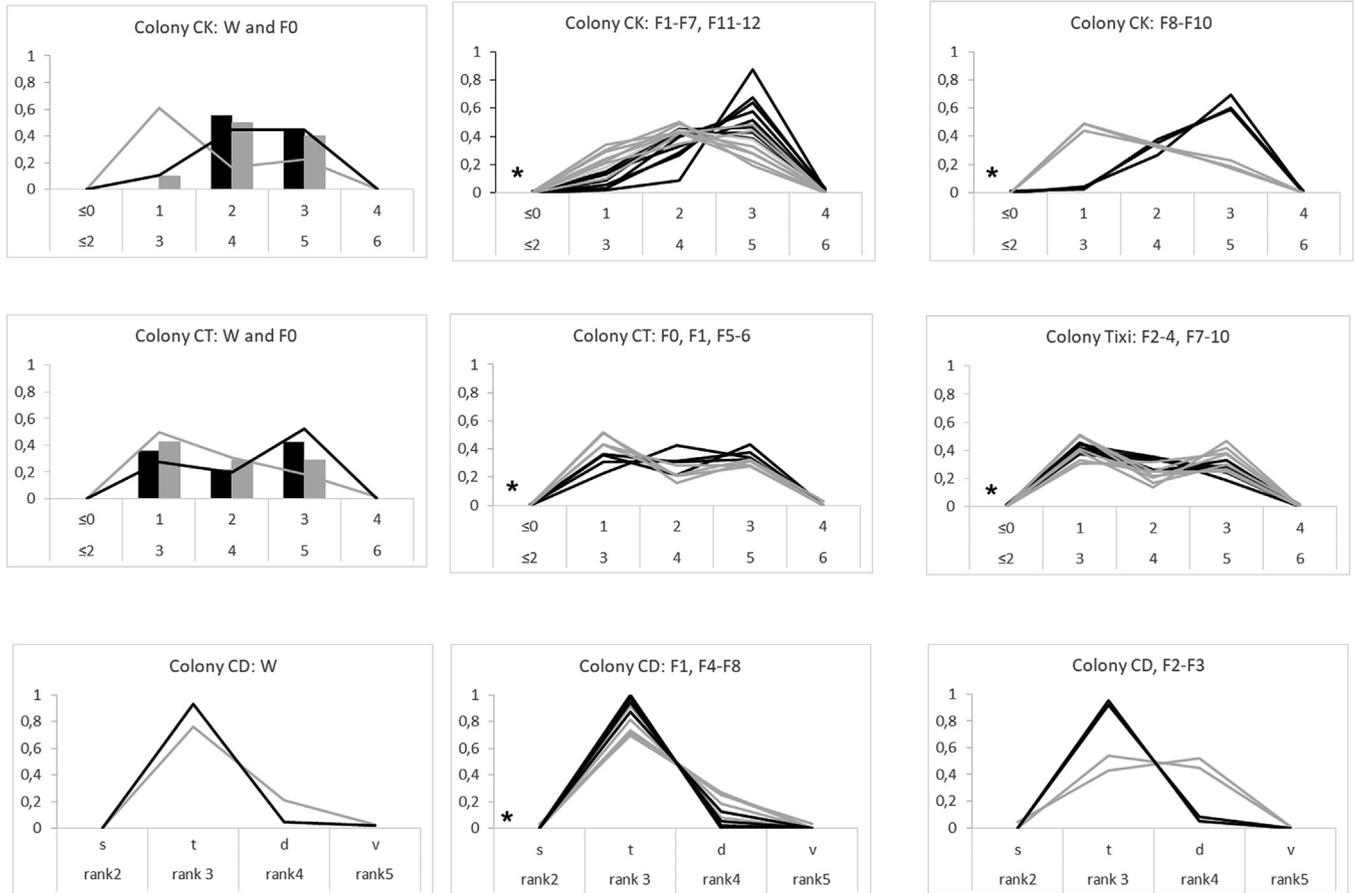
* Arvicoline terminology after Van Der Meulen, 1973

** Cricetid terminology after Reig, 1977; Maridet, Ni, 2013

Appendix A. Correspondence of dental terms used in this study to the traditional terminologies utilised in the practice of arvicoline-based Quaternary biochronology (A.1, A.2), in the studies of modern population dynamics (A.3), and in comparative morphological studies in Arvicolinae and Cricetidae (A.4).

Cluster 1

Cluster 2

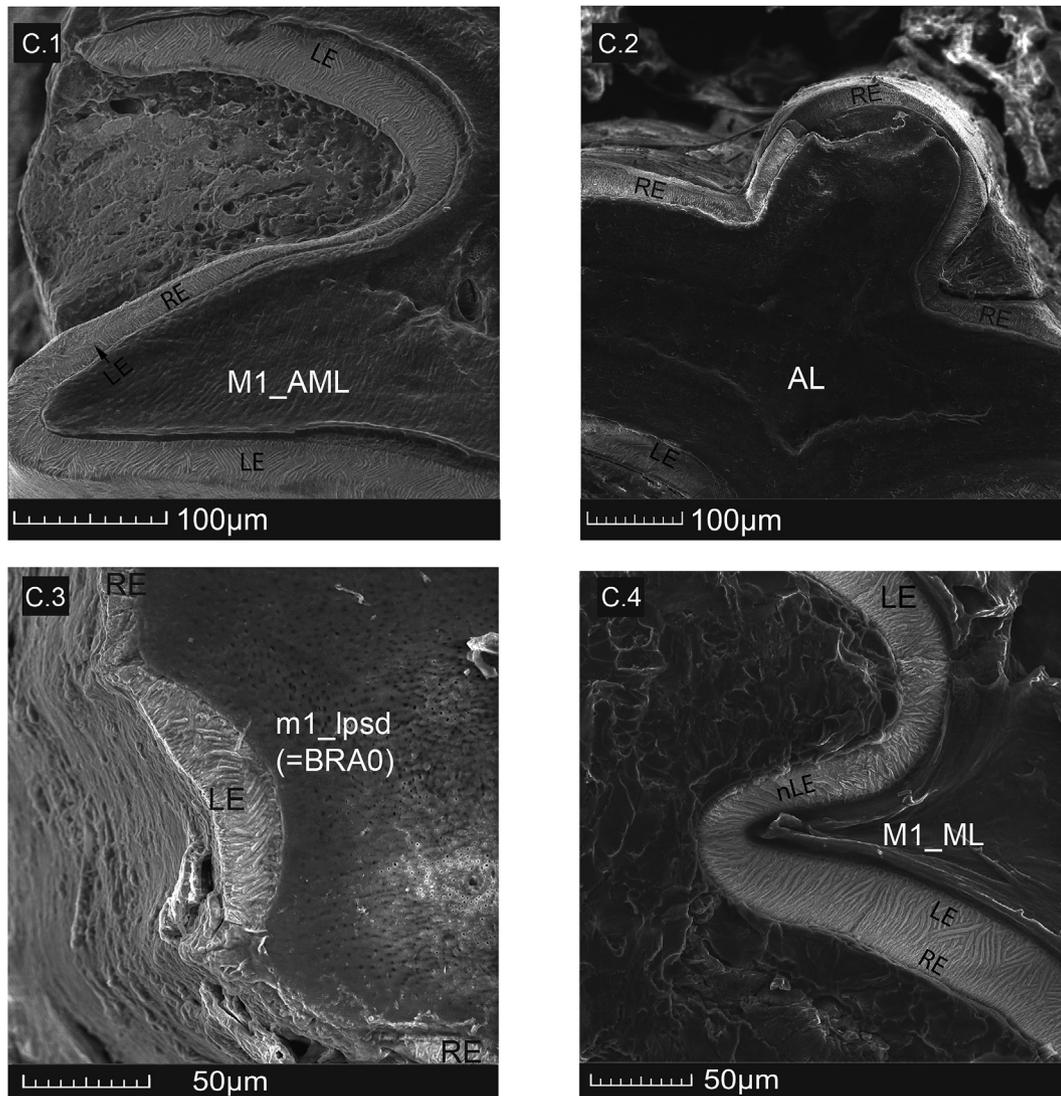


m1 Columns - founders, F0;

M3 lines - natural populations (w) or lab generations (F1-F12)

 * - simplified outliers

Appendix B. Dynamics of the frequencies of dental complexity ranks in laboratory colonies of *D. torquatus* (CK, CT) and *M. (a.) obscurus* (CD). Complexity ranks (or abbreviations of respective morphotypes) of M3/m1 are shown below x-axes; y-axes represent frequencies. See Fig. 1 for ranks and morphotypes and Fig. 2 for interpretation of clusters 1–2.



Appendix C. Enamel microstructures in the aberrant teeth of laboratory-bred *Microtus* (C.1–C.3) and naturally occurring *Dicrostonyx* (C.4). C.1 – *M. (a.) obscurus*, CD, female C8231 showing a supernumerary prism in place of anteromesoloph (M1_AML); C.2 – *M. (a.) obscurus*, CD, female C7293 showing a trilobed pattern of AL on M1; C.3 – *M. (a.) obscurus*, CD, female 7647 showing an incipient BRAO (= incipient m1_lpsd); C.4 – *D. torquatus*, locality d6, M1 with mesoloph (M1_ML). Enamel types: LE – lamellar, RE – radial, nLE – non-typical lamellae.

Appendix. DSupplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.quascirev.2019.106045>.

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