



Late Pleistocene to recent survival of true lemmings (*Lemmus*, Cricetidae) across the Palearctic revealed by modern and ancient mitogenomes

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Abstract

The analysis of mitochondrial genomes from an expanded sample of *Lemmus* across its Palearctic range, including Late Pleistocene specimens from eastern regions representing multiple time points, refines our understanding of the genus' evolutionary history in the context of climatic oscillations over the last 50,000 years. Contrary to previous studies but consistent with paleogeographic expectations, we detected significantly higher genetic diversity in non-glaciated areas than in formerly glaciated regions. Our results do not support synchronous repeated turnovers across Western Eurasia during the Late Pleistocene. Instead, haplotypes shared among sites persisted across multiple temporal intervals. Most ancient samples clustered on basal branches of the species complex, as anticipated, though some haplotypes persisted over time. The data support post-LGM colonization of Scandinavia and the Kola Peninsula, most likely during the Late Dryas. Temporal analysis of mitochondrial haplotypes indicates the combined effects of genetic drift and bottlenecks, consistent with the extremely low haplotype and nucleotide diversity observed in contemporary Norwegian lemming populations. In contrast, high genetic diversity in eastern Siberian populations suggests long-term demographic stability and prolonged persistence. Pre-LGM and LGM specimens cluster with their respective geographic clades among modern samples, further supporting this interpretation. The well preserved Yakutian mummy, the oldest studied specimen dated forty thousand years ago, possessed highly divergent haplotype and its basal phylogenetic placement, considered alongside the antiquity of the specimen, could be consistent with the retention of ancestral polymorphism predating the major split in Eurasian lemmings or may represent a previously unrecognized and now extinct lineage. Distinguishing between these scenarios will require genome-wide nuclear data and expanded sampling of temporally stratified ancient material.

Keywords Ancient DNA · Extinction · Phylogeography · Arctic · LGM

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Introduction

An increasing volume of research indicates that Late Pleistocene climatic and environmental oscillations played a decisive role in shaping the evolutionary pathways of diverse mammalian species (Shapiro et al. 2004; Blois et al. 2010; Prost et al. 2010; Lorenzen et al. 2011; Li et al. 2025; Suzuki 2026). In the Northern Hemisphere, these shifts induced substantial demographic and genetic transformations, frequently resulting in the loss of entire lineages and species or in extensive, rapid alterations of their geographic ranges.

Among small rodents one of the most informative animals to study the role of these oscillations in shaping the evolutionary trajectory is brown or true lemmings (genus *Lemmus* Link, 1795). The modern geographic range of the genus is circumpolar and extends from northern Scandinavia to the western shores of Hudson Bay and Baffin Island where it inhabits flat and mountain tundra and forest-tundra, and even open wetlands in the northern part of the forest taiga zone (Gromov and Polyakov 1992). However, fossil remains of the genus dominate in continental sediments throughout the entire Pleistocene therewith the southern border of the range during glacial periods reached France, Romania (Terzea 1972; Janossy 1986; Chaline et al. 1989) in Europe and stretched as far to the south from the present-day distribution as Mongolia (Devyatkin and Zazhigin 1974). Thus, during the last 2.5 million years the genus geographic range has repeatedly contracted and expanded. These cycles inevitably caused local extinctions and loss of genetic diversity acting as an evolutionary driver, promoting the formation of new diversity through population isolation and subsequent differentiation. Thus, Pleistocene climatic fluctuations influenced species and genetic diversity through time both positively and negatively.

Previous studies on mitochondrial cytochrome *b* (mt *cytb*) sequences (Fedorov et al. 1999; Abramson et al. 2008; Abramson and Petrova 2018) have identified two main branches. The first one corresponds to *Lemmus trimucronatus* Richardson, 1825 whose geographic range covers mainly the arctic tundra of North America and in Palearctic it is distributed from western shore of the Bering Sea to the east shore of the Kolyma River. Representatives of the second branch occur only in Palearctic and are further divided into four mt lineages. These lineages of the Palearctic group do not correspond entirely to the conventional taxa of the genus. The part of Siberian lemming, *Lemmus sibiricus* Kerr, 1792 geographic range west to the Lena River forms sister clade to the Norway lemming, *L. lemmus* Linnaeus, 1758, forming the so-called “western” lineage, while the eastern part is sister to the Amur lemming, *L. amurensis* Vinogradov, 1924 and represents the so-called “eastern” lineage. Thus, *L. sibiricus* appeared to be paraphyletic on

the mt tree. Despite the fact that the aforementioned studies were based solely on the analysis of fragments of mt *cytb*, and that numerous examples of incongruence between mt and nuclear phylogenies (e.g., de Jong et al. 2023) demonstrate how risky it is to draw taxonomic conclusions from a single non-recombining locus such as mtDNA, a number of authors nevertheless hastily proceeded to revise the taxonomic structure of the genus based on these data (Lissovsky et al. 2019, 2025; Kryštufek and Shenbrot 2021) and started to consider only two valid species in the genus: *L. trimucronatus* and *L. lemmus*, the latter covering the territory from Scandinavia up to Kamchatka Peninsula including and adjacent islands. This vast territory is currently highly fragmented preventing free gene flow between populations. First of all, *L. lemmus* in its conservative boundaries covering Scandinavia and Kola Peninsula, is separated by White Sea from the lemmings inhabiting the tundra on the East. Then, *L. amurensis* is a Pleistocene relict, possibly already extinct, located far south to the rest of the *Lemmus* area. An isolated population of the Siberian lemming occurs on the eastern coast of Kamchatka, where it is separated from the main range of the species by populations of *L. trimucronatus* (Abramson and Petrova 2018). Taking the above into account, and pending a comprehensive analysis of genomic data, we will adhere to the traditional taxonomic structure of the genus, recognizing three species of the genus in the Palearctic (Jarrell and Fredga 1993; Musser and Carleton 2005).

It is important to emphasize here that the phylogeographic structure described above was based on the study of not only a small fragment of mtDNA but also a small number of samples that do not cover most parts of the geographic range. Thus, the history of the formation of the modern genus structure and phylogenetic relationships of most populations remain poorly understood. Notably, pioneering contributions using ancient DNA (aDNA) from *Lemmus* samples (Lagerholm et al. 2014; Lord et al. 2025) significantly advanced understanding of the evolutionary history of this genus, but they analysed mostly data from western regions. These studies have shown, in particular, that in the European part of the species’ range, mt lineages existed during the Late Pleistocene that did not persist into the present. In contrast, Late Pleistocene localities in the Asian part of the range remain largely unstudied, and, as suggested by Stojak and Jędrzejewska (2022), populations in Europe and Asia may have responded differently to Pleistocene climatic fluctuations.

Summing up all above, the precise sequence of events leading to the modern phylogeographic structure remains erased, because of loose sampling, especially from Asia, and the analyses of only short fragments of mt sequences, except Lord et al. (2025). Taking into account the markedly

different environmental conditions that characterized western and eastern Eurasia during the Late Pleistocene, we hypothesize that the evolutionary and demographic histories of lemming populations in these regions — as well as their levels of genetic variation — differ substantially. We further propose that the absence of regional differences in genetic diversity reported by Fedorov et al. (1999) may reflect methodological limitations, specifically small and geographically unrepresentative sample sizes and the use of short mt sequence fragments, rather than genuine biological patterns. Here, we aimed to reconstruct the Late Pleistocene evolution and phylogeographic history of *Lemmus* genus by means of complete mitochondrial genome (mitogenome) analyses of expanding sampling from the whole Palearctic area using museum collections and including Late Pleistocene specimens from the territory of Eastern Siberia and Primorsky Krai that was not covered by paleogenomic studies.

Materials and methods

Sampling

In total, 151 true lemmings from 75 localities throughout the genus geographic range were included in the molecular

analysis (Table S1). New mitogenomes from 32 specimens were obtained within the framework of the current study (Table S2). 15 fresh samples were stored as muscle tissues in 96% ethanol in the tissue collection in the Laboratory of Evolutionary Genomics and Paleogenomics Zoological Institute RAS, St-Petersburg. 13 museum specimens (collected in 1883–1994) were stored as skins in the voucher collection of the Laboratory of Theriology, ZIN RAS, see Table S2 for details.

Four Late Pleistocene samples were included in the analysis. Three mummies (Fig. S1) were found in North-East Yakutia (Fig. 1, locs. 55, 56). The mummified specimen from Tirekhtyakh River (Fig. 1, loc. 56) stored in Paleontological Institute RAS, Moscow (PIN RAS, voucher 5663/1) was thoroughly studied by Lopatin et al. (2019), it was C-14-dated to 41.885–41.305 thousand years ago (kya).

Two specimens from permafrost-preserved lemming tissues (Ns. 6346, 6347) from the same region, Ogorokha River (loc. 55), stored in the Academy of Sciences of the Republic of Sakha (Yakutia), were selected for collagen extraction from bone and fur, followed by AMS radiocarbon dating. Sample preparation and processing were performed at the Core Facility “CenozoicGeochronology” of the Institute of Archaeology and Ethnography, Siberian Branch of the Russian Academy of Sciences. AMS analysis was

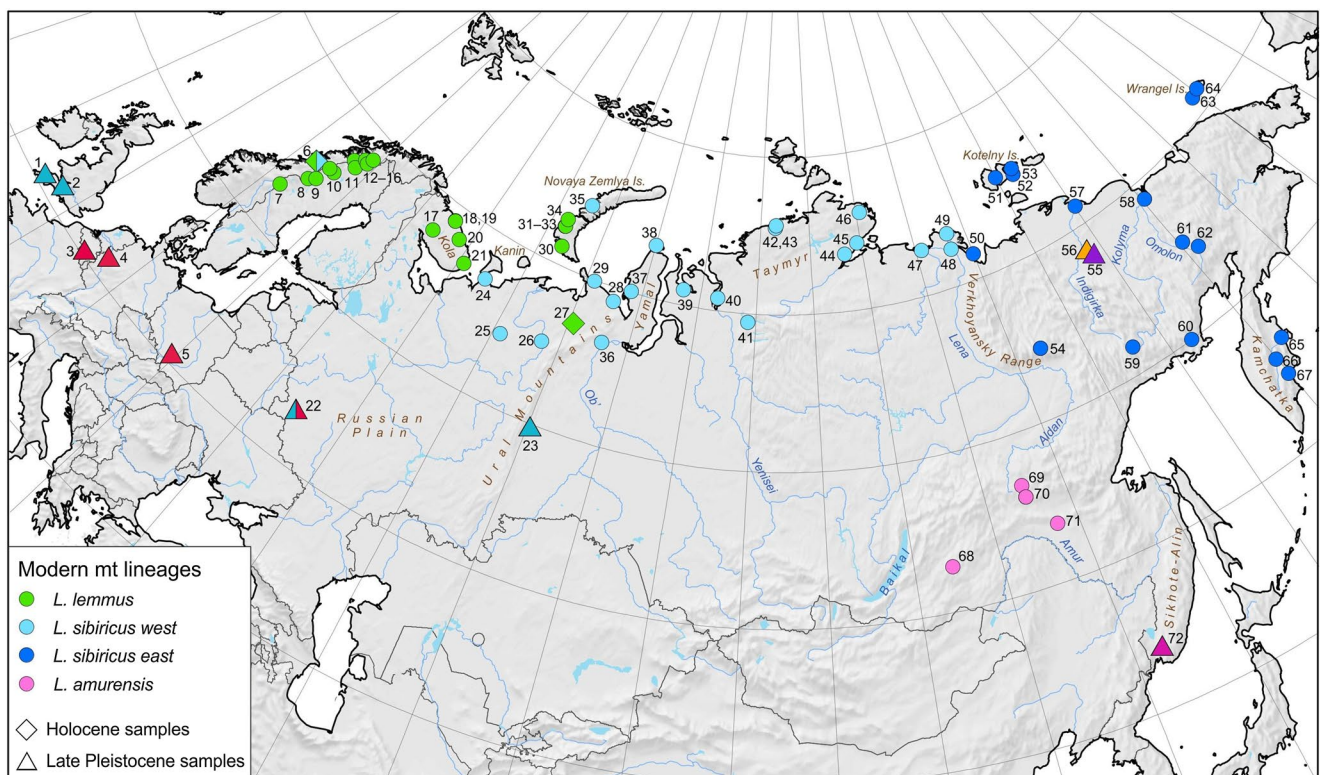


Fig. 1 Material used in the study. Modern samples indicated by circles are coloured according to cytochrome *b* lineages (green, light blue, blue and pink for modern *L. lemmus*, *L. sibiricus* west and east and *L.*

amurensis, respectively). Holocene and Late Pleistocene samples are indicated by diamonds and triangles respectively and coloured according to the *cytb* tree. Locality numbers correspond to Table S1

conducted at the AMS Golden Valley Core Facility, Novosibirsk State University, using the MICADAS-28 instrument with the AGE-3 graphitization system. Samples were dated as 31.280–29.733 and 21.116–20.614 kya.

One fossil specimen, represented by a tooth, was excavated from Perspektivnaya cave (Fig. 1, loc. 72) in Primorsky Kray, Southern Sikhote-Alin Ridge. *Lagopus lagopus* sample from the same layer in this site was C-14-dated as 18.610–18.490 kya (Beta-660120) by Beta Analytic Inc. (Miami, Florida). *Lemmus*' sample also was referenced on this date.

DNA extraction, library preparation and sequencing

We conditionally divide the samples into fresh (collected after 2000 and fixed in 96% ethanol), historical dry museum tissues (pieces of dried skin were taken mainly from the inner side of the lip) collected in 1883–1994) and ancient ones (four samples dated to the Late Pleistocene). The DNA extraction from modern and historical samples was performed using phenol-chloroform method according to protocols (Barnett and Larson 2012; Green and Sambrook 2017). DNA concentrations were measured using the QuDye ssDNA Assay Kit (Lumiprobe, RUS Ltd, Russia) with a Qubit v.4.0 fluorometer (Thermo Fisher Scientific, CA, USA). Genomic libraries for modern and museum specimens were performed by MGI company (MGI Tech Co Ltd., Shenzhen, China).

The aDNA extraction was conducted in the clean laboratory of evolutionary genomics and paleogenomics at the Zoological Institute RAS in St. Petersburg, Russia. We ground teeth and jawbones using porcelain mortar and pestle. After grinding each sample, we cleaned the PCR box and instruments using bleach, ethanol, and UV light for 10 min. The aDNA extraction was performed using a silica-based method proposed by Rohland and Hofreiter (2007) with modifications described by Panitsina et al. (2023). The Allsheng Fluo-200 Fluorometer (Hangzhou Allsheng Instruments Co., Ltd., Hangzhou, China) was used for measurement of DNA concentrations. We measured the length of the extracted DNA using the TapeStation 4150 System with the High Sensitivity D1000 ScreenTape assay (Agilent Technologies, Santa Clara, CA, USA). Due to the low DNA concentration, the Perspektivnaya cave sample's genomic library was prepared with the Ovation® Ultralow Library System V2 kit (Tecan Group Ltd., Männedorf, Switzerland) according to the manufacturer's instructions. Genomic libraries for three ancient samples from North-East Yakutia were prepared using the KAPA HyperPlus Kits (Kapa Biosystems, Wilmington, MA, USA) according to the

manufacturer's instructions. The purification and double size selection of NGS library fragments were done using Agencourt AMPure XP Beads (Beckman Coulter, MA, USA). NGS library concentrations were measured using the QuDye ssDNA Assay Kit (Lumiprobe, RUS Ltd, Russia) with a Qubit v.4.0 fluorometer (Thermo Fisher Scientific, CA, USA). Library quality was evaluated using the TapeStation 4150 System with the High Sensitivity D1000 ScreenTape assay (Agilent Technologies Publication: Santa Clara, CA, USA). The average library length of all samples was ~250 bp. The DNBSEQ-G400 (MGI Tech Co Ltd., Shenzhen, China) was utilized for paired-end whole-genome sequencing (2 × 150 bp) for all samples, yielding approximately 100 million paired reads per sample (Table S2).

Raw data analysis and mitochondrial genome assembly

The quality of raw reads was evaluated in FastQC ver. 0.11.934 (Andrews 2010), then reads were rid of Illumina adapters, overrepresented sequences and low-quality reads (<Q20) using Trimmomatic v0.3935 (Bolger et al. 2014). Testing for damage patterns in aDNA sequences (postmortem damage such as hydrolytic deamination of cytosine and adenine at 5'-ends and 3'-ends of DNA strand, respectively) was carried out with DamageProfiler software (Neukamm et al. 2021). Metagenomic analysis is used to evaluate the amount of endogenous DNA, besides surveying microbial diversity in ancient samples. Kraken 2 software (Wood et al. 2019) was used to determine the taxonomic rank of the raw reads, while Krona (Ondov et al. 2011) and Pavian (Breitwieser and Salzberg 2020) were used for visualization and sample comparison. We classify all reads that are mapped to Rodentia, not solely to *Lemmus sp.*, as endogenous DNA. Mitochondrial genomes were assembled in MitoZ (Meng et al. 2019) with default settings. The de novo assemblies failed for three low quality sequencing samples (№ 6320, 6359, 6360). For these samples we mapped reads to the reference mitogenome using BWA ALN (Li and Durbin 2009). Additional steps such as sorting, filtering and duplicate removal were provided with Samtools software (Li et al. 2009). Consensus was generated with samtools consensus. Multiple alignment (the Geneious multiple alignment algorithm) was realized in Geneious Prime V. 2019.2.1 (Biomatters Ltd., Auckland, New Zealand).

Phylogenetic analyses

Phylogenetic reconstructions were performed using two datasets. The first consisted of 43 complete mitogenome sequences (32 mitogenomes generated in this study, along with 11 mitogenomes retrieved from the European Nucleotide Archive, ENA). The second consisted of 151 sequences and comprised partial 76 bp *cytb* sequences concatenated with partial 95 bp D-loop sequences. This dataset incorporated fragments from 32 new mitogenomes, as well as *cytb* and D-loop sequences from NCBI GenBank. *Lemmus trimucronatus* was used as an outgroup in both cases.

Phylogenies were reconstructed by maximum likelihood (ML) and Bayesian inference (BI) analysis for both datasets. The ML analysis was carried out on the IQ-TREE Web server (Minh et al. 2020) with 10,000 ultrafast bootstrap replicates (Hoang et al. 2018). Model selection for nucleotide substitution was performed automatically by IQ-TREE during the analysis.

The BI analysis was performed in MrBayes 3.2.649 (Ronquist et al. 2012). Each analysis started with random trees and was performed as two independent runs with four independent Markov Chain Monte Carlo (MCMC) algorithms for 10 million generations with sampling every 1,000th generation; the first 25% of the sampled trees were discarded as burn-in. Stationarity was examined in Tracer v1.7.2 (Rambaut et al. 2018). Instead of selecting a specific substitution model for each gene or partition, automatic model selection was performed using the MrBayes command `lset nst=mixed rates=invgamma`.

Divergence dating

Due to the low resolution of the short fragments (partial *cytb* and D-loop), we used only complete mitogenomes for divergence dating. We examined two approaches to divergence dating. Initially, we constructed a tree based on data derived from ancient samples. Tip dates were set as mean values for five specimens – Bridged Pot, loc. 2 (12.573 kya) and Pymva Shor, loc. 27 (9.655 kya) published by Lord et al. (2025), and four obtained in the current study: Tirekhtyakh River, loc. 56 (41.599 kya), Ogorokha River, loc. 55 (two specimens – 18.972 and 28.390 kya) and Perspektivnaya cave, loc. 72 (18.550 kya). The second analysis also included data about the divergence time between *L. trimucronatus* and Palearctic branch of true lemmings. We set a minimum divergence age of 2 million years, assuming the populations were continuous approximately until that time and became isolated thereafter with warming that was recognized throughout the Northern Hemisphere close to 2 Mya (Funder et al. 1985). This value represents the

probable onset of divergence rather than the precise time of species origin. This estimate is approximate, as speciation is gradual, and *L. trimucronatus* remains morphologically indistinguishable from *L. sibiricus*.

Estimates of divergence times among taxa were calculated using BEAST v2.7.8 software (Bouckaert et al. 2019). To select the most suitable substitution models, we employed BEAST Model Test v1.3.3 (Bouckaert and Drummond 2017) with the comprehensive “allreversible” model set and frequencies estimated from the data. We applied an optimized relaxed clock model v1.2.1 (Douglas et al. 2021) combined with the fossilized birth–death (FBD) process as tree priors. For the FBD model, we set the time of origin to 10 million years (estimate). Standard parameters were utilized to specify the clock model’s priors. For the diversification rate under the FBD model, we used an exponential prior with a mean of 0.1 and an offset of 0. The most recent common ancestor (MRCA) of *Lemmus* genus was calibrated with a normal prior distribution on the root height, characterized by a mean of 2.0 and a standard deviation (SD) of 0.2 million years.

The MCMC analysis was run with a chain length of 100 mln generations for two independent chains, sampling every 10,000 generations. Stationarity and convergence were assessed using Tracer v1.7.2 (Rambaut et al. 2018). Afterward, the tree files from both chains were combined using LogCombiner v2.7.8 discarding the first 10% as burn-in. The combined trees were annotated with TreeAnnotator v2.7.8 (Heled and Bouckaert 2013), which summarizes the posterior sample into a consensus tree. This consensus tree was visualized using FigTree v1.6 (<http://tree.bio.ed.ac.uk/software/figtree/>, accessed on 26 November 2021), and divergence time intervals were automatically generated based on the 95% highest posterior density (HPD) intervals for each node.

Haplotype network construction

For phylogenetic reconstruction, we concatenated *cytb* and D-loop sequences. However, to explore spatial and temporal patterns of genetic variability and haplotype relationships, we expanded the dataset based on the mt *cytb* fragment and did not include data from the D-loop region. Owing to its high variability, the D-loop may introduce additional noise and potentially lead to an overestimation of haplotype numbers, especially when analyses are performed across the species’ entire range rather than at a local geographic scale. Thus, while D-loop is valuable for phylogeny (providing polymorphic sites to resolve branches and avoid polytomies), it is less suitable for haplotype network resolution. To construct the haplotype network and estimate genetic diversity, we used a 305 bp *cytb* fragment (136 samples).

Ambiguous sites were removed from the alignments prior to haplotype inference. A temporal haplotype network was constructed using the TempNet script (Prost and Anderson 2011) implemented in R version 4.2.3 (R Core Team, 2022, Vienna, Austria) with minor modifications. The dataset was divided into three temporal groups corresponding to distinct intervals: Late Pleistocene (48–26.5 kya), Last Glacial Maximum (LGM) and post-LGM (26.5–11 kya), and modern to Holocene (11 kya to present). The lower boundary of the LGM is established at 26.5 kya (Clark et al. 2009). Indices of haplotype (Hd) and nucleotide (Pi) diversity, along with their standard deviations, were calculated for the eastern and western groups of lemmings, and specifically for *L. lemmus*, *L. sibiricus* west, *L. sibiricus* east, and *L. amurensis* using DnaSP V6.12.03 (Rozas et al. 2017).

Results

Mitochondrial genome sequencing and assembly

We sequenced and assembled mitogenomes from 28 modern lemming specimens as well as from four ancient ones. Mostly mitogenomes were complete (16,328–16,346 bp). Because sequencing depth was high, the relatively low endogenous DNA content in these ancient samples still allowed reconstruction of complete or near-complete mitogenomes with negligible gaps. Only two modern specimens (taken from museum tissues, collected in 1932) and one ancient specimen (18.6 kya) mitogenomes were partial (11,434–16,209 bp), see Table S2 for details.

The analysis of damage patterns (Fig. S2) revealed a low variation in the values of deamination misincorporations (between approximately 1 and 7%, Table S2). In the analysis we observe C-to-T and G-to-A substitutions at the ends of the sequences for two samples, *L. amurensis*, Perspektivnaya cave, 18.6 kya, and *Lemmus* sp., Tirekhtyakh River, 41.6 kya.

The assembly quality is shown in Table S2. The total number of reads varies from 12.1 to 343 million bp for modern samples and from 91 to 406.3 million bp for ancient ones. Duplicates percentage ranging from 6.2 to 48 for modern and from 6.2 to 53.9 for ancient samples.

Metagenomic analysis

The mitogenome descriptive statistics are provided in Table S3; additionally, we present pie charts for all specimens for clarity (Fig. S3). We calculated the percentage of classified and unclassified reads, which represent the fraction of sequences having homologous sequences in GenBank NCBI. The percentage of classified reads varied from

45.70 to 99.70% for ancient specimens. The percentage of rodent reads varies from 2.04 to 99.08. The minimal value of endogenous DNA, 2.04%, belongs to the ancient sample from Perspektivnaya cave dated to 18.550 kya. Analysis of two samples from Ogorokha River reveals a significantly high percentage of endogenous DNA.

Phylogenetic relations, divergence time's estimates and genetic diversity

To estimate phylogenetic relationships of lemming populations through time and space we used two datasets, one including complete mitogenomes with a limited sample on specimens used in the current study and the enlarged one combining short fragments of mt *cytb* and D-loop with previously published sequences of fossil lemmings from Europe. The trees produced from both datasets in all kinds of analyses (Figs. 2 and 3, S4) demonstrate the division of all studied Palearctic lemmings' populations into two main branches as reported by previous studies. The first one, so-called "western" lineage, unites modern lemmings conventionally assigned to *L. lemmus*, and lemmings east of the White Sea and up to the Lena River. The second one, "eastern" unites lemmings east of the Lena River and up to the Kamchatka Peninsula, and a clade of populations conventionally assigned to *L. amurensis*.

The tree produced from the enlarged dataset and short fragments of mitogenome (Fig. 2) shows that Late Pleistocene samples from Europe, the Russian Plain, and the Urals split into two groups. The first group including only Pleistocene samples from sites in Central Europe and the Russian Plain occupies the basal position related to all the Recent and extinct lemming populations of the western lineage. The second group of Pleistocene samples from sites in the Middle Urals, some specimens from the Russian Plain and British Isles fall within the western lineage together with modern samples. Noteworthy, that at the same time, all Late Pleistocene specimens from localities in the British Isles, as well as one specimen from Studenaya Cave in the Middle Urals, form a single well-supported clade together with modern Norway lemming specimens including sample from Novaya Zemlya archipelago and Holocene-aged specimen from the Northern Urals. The majority of specimens from Middle Urals and approximately half of the specimens from the Russian Plain form separate clusters occupying independent phylogenetic position within the broader western clade uniting modern Norway lemmings and modern Siberian lemmings of the western lineage. Noteworthy is that the mummy from Yakutia, Tirekhtyakh, Middle Indigirka River (loc. 56) aged 41.6 kya in this analysis with a moderate support shows basal position to all the fossil and extant lemming clades of the western lineage described above.

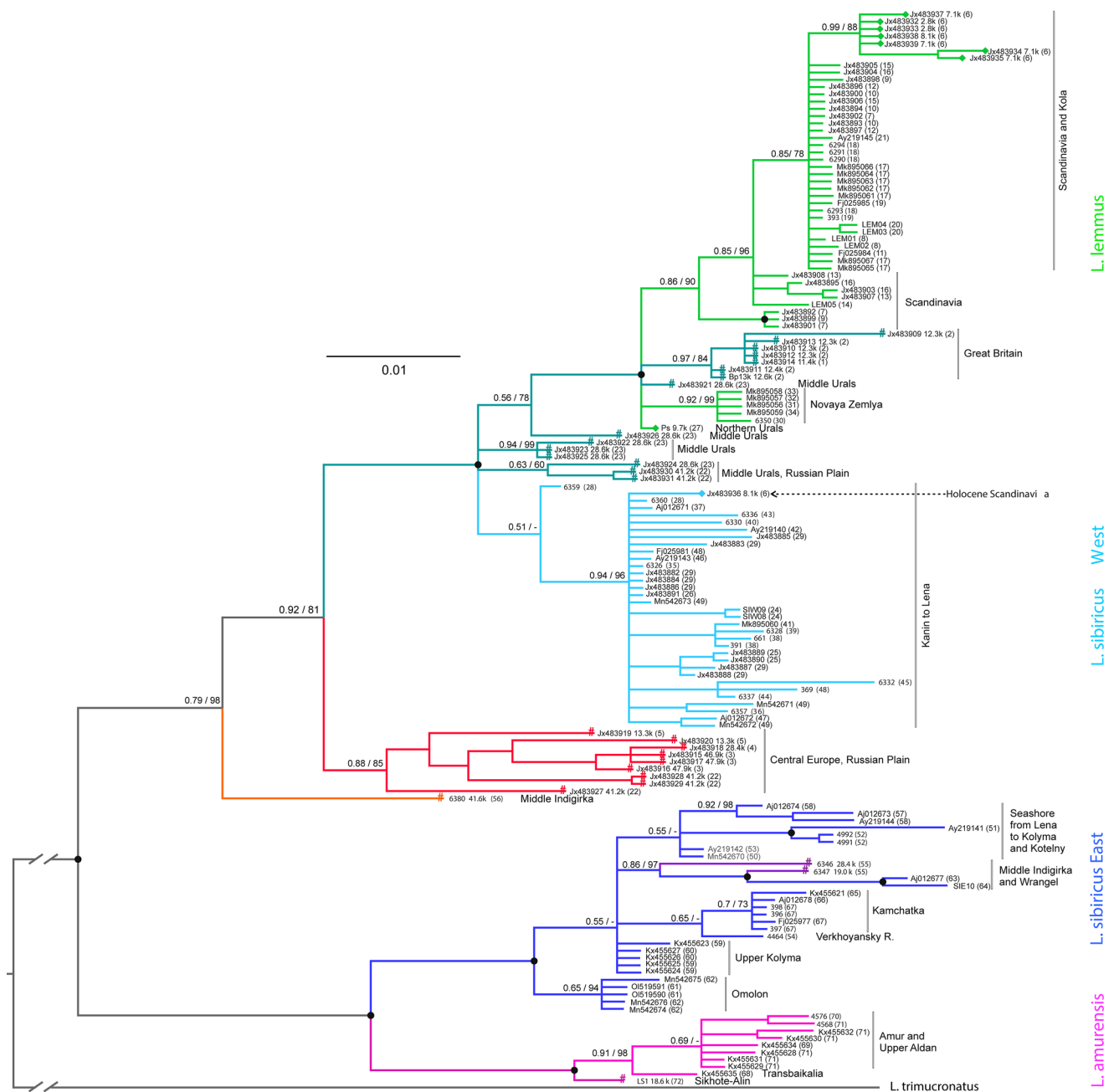


Fig. 2 Bayesian phylogenetic reconstruction of *g. Lemmus* based on *cytb* and D-loop fragments. Holocene and Late Pleistocene samples are indicated by diamonds and triangles respectively. Node labels show Bayesian posterior probability/ML bootstrap support; black

circles denote nodes with 0.95–1.0 BI and 95–100 ML support. New mitogenomes obtained are highlighted in bold. Locality IDs (in brackets) correspond to Fig. 1 and Table S1. Outgroup is collapsed for better visualisation

The eastern lineage in the analysis of the enlarged dataset splits into two main branches: the one uniting all lemming populations in North-Eastern Siberia and adjacent islands and the other one the populations of Amur lemming of South Yakutia, Eastern Transbaikalia and Amur region. The fossil Pleistocene samples from the Ogorokha River, Middle Indigirka (loc. 55) are close to the sample from the Wrangel island; and Pleistocene sample from the Primorsky

Kray, Southern Sikhote-Alin (Perspektivnaya cave), is the earliest derivative in the clade of Amur lemming.

The trees produced from the limited dataset but complete mitogenomes (Figs. 3, S4), using BI and ML methods demonstrate similar topologies with slightly different node supports. The only difference is that in the BI and ML analyses (Fig. S4) fossil mummified specimen (aged as 41.6 kya) from northern Yakutia, (loc. 56), although with low support

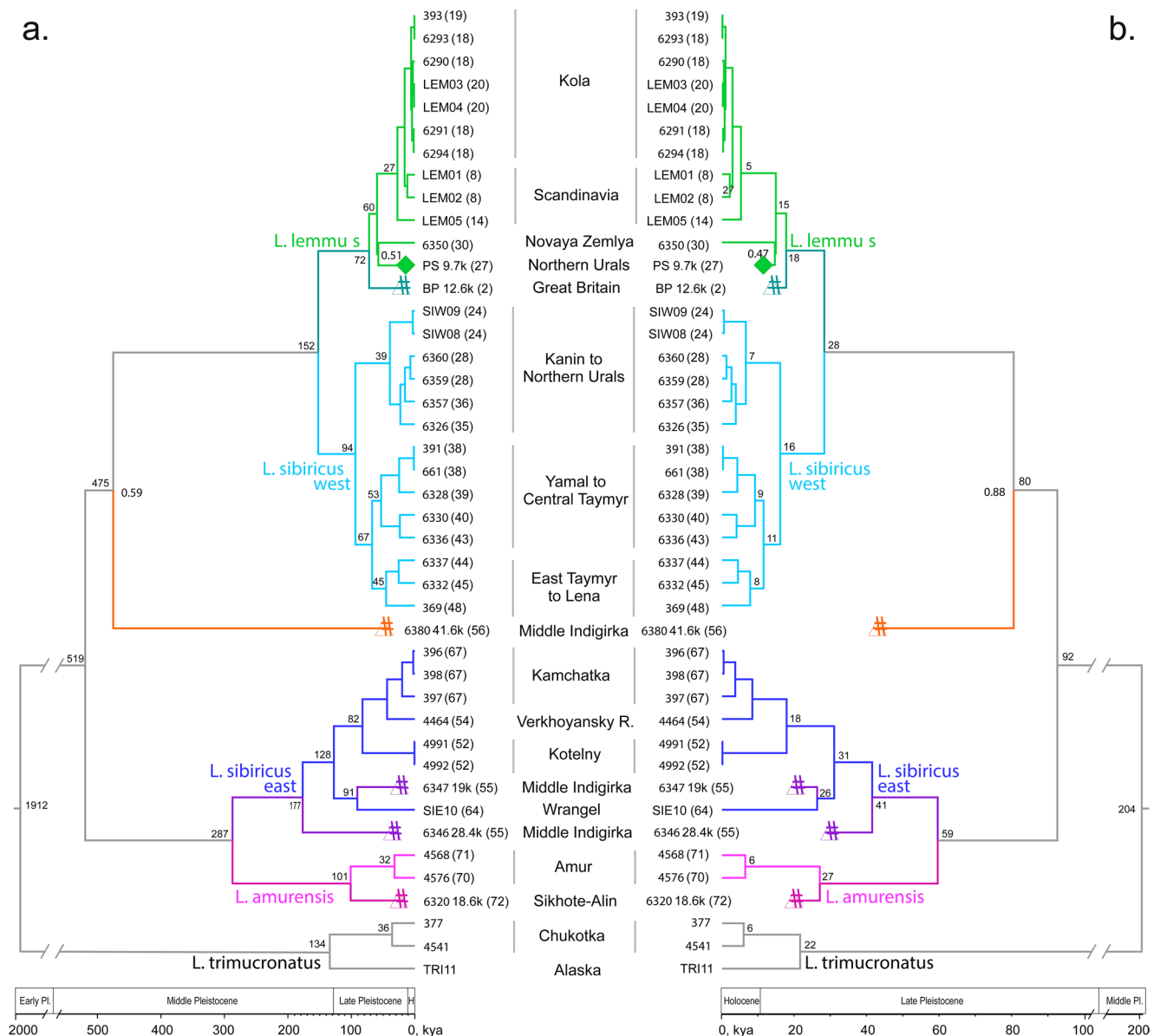


Fig. 3 The maximum clade credibility tree for *Lemmus* complete mitochondrial genomes. **(a)** Tip dates and root calibration used. **(b)** Only tip dates used. For new mitogenomes obtained tissue IDs are highlighted in bold. Locality IDs (in brackets) correspond to Fig. 1 and

Table S1. Mean dates in kya are indicated at major nodes. All Bayesian posterior probabilities are above 0.97 except the two marked in italic next to the nodes

(0.74 BI / 60% ML), appeared to be basal to the eastern group, combining mt lineages of *L. sibiricus* east and *L. amurensis*. At the same time in the maximum credibility tree in the divergence dating analysis (Fig. 3) this specimen again appears to be basal to the western branch.

Two dated trees (Fig. 3a, b) were inferred from an identical dataset using distinct calibration strategies. Incorporation of root calibration yielded substantially different age estimates compared to those obtained without it. The divergence dating analysis of complete mitogenome data, using both tip dates and root calibrations (Fig. 3a), estimated the time to the most recent common ancestor (tMRCA) of the

eastern and western lemming clades at approximately 519 kya (95% HPD 820–255). The tMRCA of western branch is estimated as ~152 (243–72) kya, the western branch further on splits into two well supported clades, one unites the all lemmings conventionally attributed to *L. lemму s*, lemmings from Novaya Zemlya archipelago and fossil lemmings from British Isles and Northern Urals. The other one unites all extant lemmings east of the White Sea up to the Lena River. The latter cluster in its turn is divided into two supported clades across the Urals. The tMRCA of the Norwegian lemming proper is estimated at around 27 kya (46–12). The tMRCA of the lemmings' populations east of

the White Sea up to the Lena River, conventionally referred to *L. sibiricus* is estimated as ~94 kya (149–45), tMRCA of the eastern branch is dated back as ~287 kya (447–136), this branch splits into well resolved *L. sibiricus* eastern lineage (its tMRCA is estimated as ~177 kya (279–86)) and lineage of lemmings conventionally referred to *L. amurensis* (with the MRCA time estimated as ~101 kya (171–45)). The Late Pleistocene specimen from Sikhote-Alin (loc. 72) is robustly placed in a basal position within the last cluster.

Divergence time estimates obtained using calibration based solely on tip dates are substantially younger (Fig. 3b). Thus, the time of divergence of *L. trimucronatus* is estimated as ~204 kya, while the primary split between the western and eastern lineages is dated to ~92 kya (119–69). According to this analysis, the oldest Yakutian sample diverged

from the western lineage at approximately ~80 kya (102–57), whereas the Norwegian lemming diverged from the West Siberian lineage at ~28 kya (36–21). The divergence time between the Amur lemming and the eastern clade of the Siberian lemming is estimated as ~59 kya (74–46).

Population structure and genetic diversity

The median-joining *cytb* haplotype network (Fig. 4) demonstrates the same clusters as at the trees but illustrates regional genetic diversity and its dynamics through time. Notably, it explicitly shows that all extant populations lineages of lemmings are separated from each other by extinct transitional haplotypes. At the same time, the network identifies a haplotype present in modern Scandinavian and Kola Peninsula

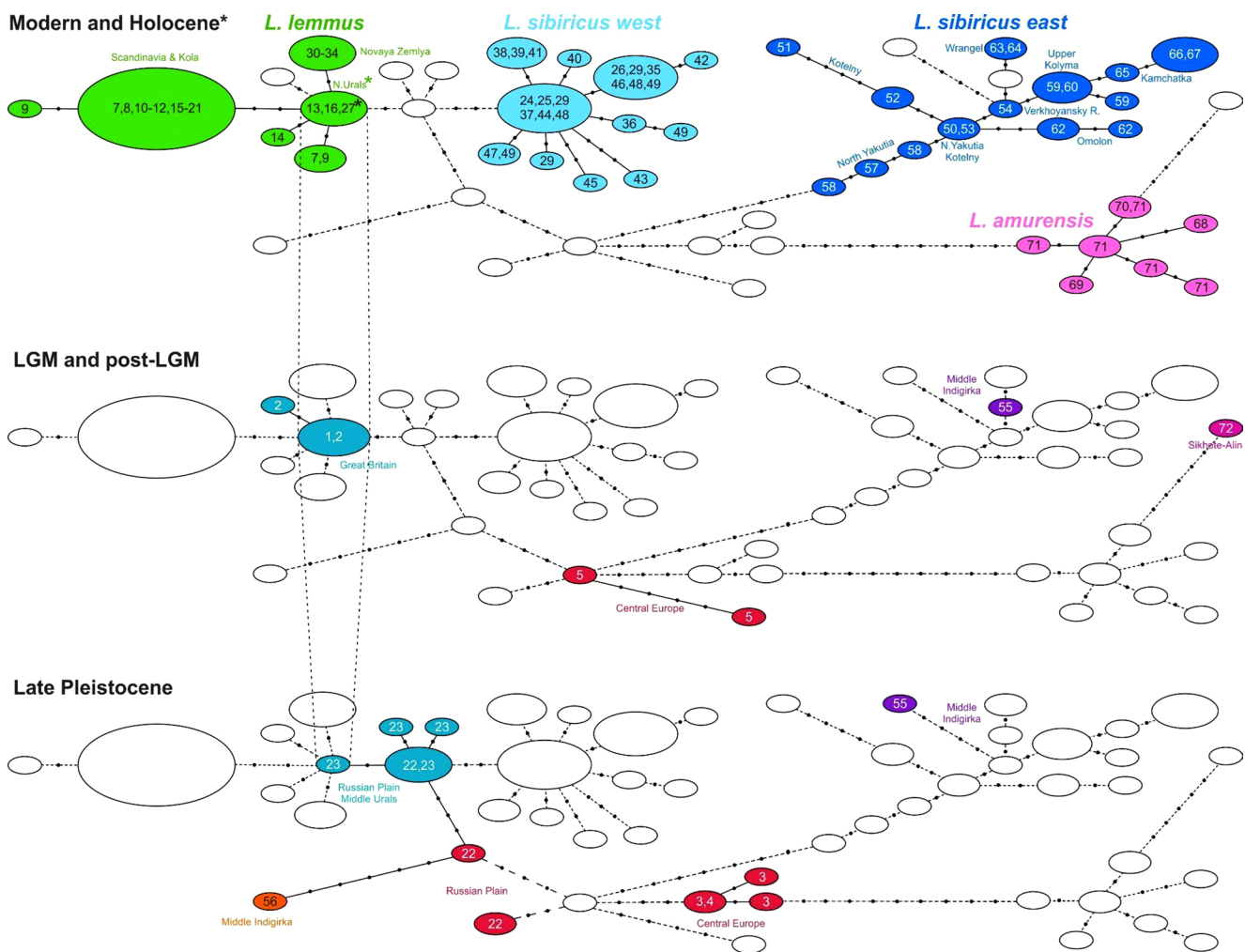


Fig. 4 Haplotype network constructed based on 305 bp cytochrome *b* fragments. Haplotypes are temporally divided into the Modern and Holocene (11–0 kya), LGM and post-LGM (26.5–11 kya), and Late Pleistocene (48–26.5 kya). The only Holocene specimen is marked with an asterisk. Ovals are coloured according to the *cytb* tree (Fig. 2) and numbered by the locality IDs (Fig. 1), empty ovals indicate hap-

lotypes that are missing in one temporal layer but are present in the other. The haplotype occurring through several periods is connected by vertical dotted lines. Black dots represent the number of nucleotide substitutions between haplotypes. The number of individuals sharing a haplotype is reflected by the oval size

lemming populations that was present in the Middle Urals prior to the LGM, became widespread in the British Isles during the LGM, and persisted into the Holocene, including the early Holocene in the Northern Urals.

Lemmings in the western Palaearctic exhibit low genetic variability ($H_d=0.86$; $P_i=0.0103$, Table 1) and a star-like haplotype structure, observed both in the lemming populations of Scandinavia and the Kola Peninsula (*L. lemmus*) and in populations east of the White Sea representing the western lineage of the *L. sibiricus*. In *L. lemmus*, the center of this star is a haplotype persisting since the pre-LGM period, from which the most common haplotype differs by only two substitutions. The genetic diversity of the Norwegian lemming ($H_d=0.556$; $P_i=0.00436$) is lower than that of the other three mt lineages. In the western lineage of the Siberian lemming, two haplotypes are dominant and occur in multiple localities from the Northern Urals to the mouth of the Lena River; one of these haplotypes is also present in the Novaya Zemlya, Northern Island population. The genetic diversity of the western lineage of *L. sibiricus* ($H_d=0.828$; $P_i=0.00487$) is slightly higher than that of *L. lemmus*.

Modern populations of the eastern lineage exhibit high genetic variability ($H_d=0.967$; $P_i=0.02276$, Table 1) and lack a star-like haplotype structure. The same applies to the eastern lineage of *L. sibiricus*, which has slightly lower haplotype and nucleotide diversity ($H_d=0.943$; $P_i=0.01115$) than the entire eastern lineage. Both fossil specimens from the Ogorokha River, Middle Indigirka (loc. 55) fall within this haplogroup. The specimen dated to 28.4 kya differs only slightly from modern specimens, whereas the specimen dated to 19 kya is virtually indistinguishable from modern representatives. At the same time, the haplotype of a mummified lemming specimen from the same area (loc. 56) dated to 41 kya shows no association with the eastern Siberian lemming haplogroup and instead is affiliated with the haplogroup of extinct Late Pleistocene lemmings from the Russian Plain and Western Europe.

The Amur lemming haplogroup is not connected to haplotypes of the east siberian lineage, whereas the closest haplotypes to the Amur lemming derive from extinct lemmings

in Western Europe sites, dated to 46 and 28 kya. A fossil specimen from the Southern Sikhote-Alin (Perspektivnaya cave) dated as 18.6 kya undoubtedly belongs to the Amur lemming haplogroup, though distant from modern haplotypes. Despite the small sample size, the genetic diversity of the Amur lemming is quite high ($H_d=0.956$; $P_i=0.00911$).

Discussion

The novelty of our study lies in the comprehensive sampling of the genus *Lemmus* across its entire Palearctic distribution. It includes not only modern specimens' data, but also ancient samples from eastern regions with several time points from the Late Pleistocene. In addition to incorporating extensive and previously unpublished material from across the Palearctic region, we also introduced minor modifications to the analytical framework and the dataset employed in earlier studies (Lagerholm et al. 2014; Lord et al. 2025).

We also incorporated additional calibration points into the divergence time analysis. For two fossil specimens from Ogorokha, the results were somewhat ambiguous: radiocarbon dating yielded ages of 19 and 28.4 kya, whereas damage pattern analyses did not reveal the typical signatures of ancient DNA degradation, and metagenomic analysis indicated a very high proportion of endogenous DNA. It is worth noting that these specimens were recovered from permafrost deposits. From nearby localities, considerably older mammoth remains have been studied, from which even RNA was successfully recovered (Mármol-Sánchez et al. 2026). We interpret the atypical DNA quality metrics observed in the Ogorokha specimens as a consequence of exceptional preservation. On this basis, we include these two dates as calibration points in the divergence time analysis alongside the other fossil calibrations.

Lord et al. (2025) estimated the time of separation of *L. trimucronatus* from the Palearctic branch of true lemmings as ~250 kya. Such a late estimate of this split is inconsistent with the paleontological record. The oldest remains of forms morphologically very close to genus *Lemmus* are known from the Early Pliocene sites of Europe (Sukhov 1976; Kowalski 1977; Abramson and Nadachowski 2001), North Mongolia (Devyatkin et al. 1989), north-eastern Asia (Zazhigin 1997) and North America (Repenning et al. 1987), evidencing for transcontinental range of *Lemmus* at ca. 2.6–2.1 Mya. Therewith the fossil remains in Western Palearctic appear to be slightly older than lemmings from the Kolyma and Alaska (Repenning et al. 1987). Morphologically very similar and nearly contemporaneous (beginning of Early Pleistocene, late Blancan) lemmings from the latter sites mark the opening of the Beringian dispersal corridor (Tesakov and Bondarev 2022). The subsequent warm

Table 1 Genetic diversity within the major cytochrome *b* lineages of Palearctic true lemmings

	<i>N</i>	<i>H</i>	<i>U_h</i>	$H_d \pm SD$	$P_i \pm SD$
Western Palearctic	89	21	12	0.860 ± 0.026	0.01030 ± 0.00047
<i>L. lemmus</i>	43	6	2	0.556 ± 0.082	0.00436 ± 0.00062
<i>L. sibiricus</i> west	31	11	7	0.828 ± 0.046	0.00487 ± 0.00076
Eastern Palearctic	37	24	16	0.967 ± 0.016	0.02276 ± 0.00217
<i>L. sibiricus</i> east	27	16	10	0.943 ± 0.027	0.01115 ± 0.00147
<i>L. amurensis</i>	10	8	6	0.956 ± 0.059	0.00911 ± 0.00249

N – sample size; *H* – number of haplotypes; *U_h* – number of unique haplotypes, H_d – haplotype diversity; P_i – nucleotide diversity; *SD* – standard deviation

Table 2 Divergence time estimates for major lineages within the *Lemmus* genus

MRCA	Mean time [95% HPD], kya		Abramson and Petrova 2018	Lord et al. 2025
	Current study	Tip dates only		
	Root & tip dates			
Nearctic / Palearctic	1912 [2117–1714]*	204 [300–106]	2148 [2585–1106]	247 [343–175]
<i>L.l.</i> , <i>L.s.w./L.s.e.</i> , <i>L.a</i>	519 [820–255]	92 [119–69]	1055 [1066–372]	124 [172–89]
<i>L. lemmus/L. sibiricuswest</i>	152 [243–72]	28 [36–21]	310 [352–101]	34 [45–25]
<i>L. lemmus</i>	72 [115–34]	18 [21–15]		19 [24–16]
<i>L.l.</i>	60 [96–28]	15 [18–12]		16 [20–13]
modern+holocene				
<i>L.l.</i> modern mainland	27 [46–12]	5 [7–3]		6.4 [8.1–4.4]
<i>L. sibiricuswest</i>	94 [149–45]	16 [21–11]		
Middle Indigirka	475 [673–200]	80 [102–57]		
<i>/L. l. +L. s. w</i>				
<i>L. sibiricuseast</i>	287 [447–136]	59 [74–46]	679 [740–206]	
<i>/L. amurensis</i>				
<i>L. sibiricuseast</i>	177 [279–86]	41 [49–34]		
<i>L. amurensis</i>	101 [171–45]	27 [33–22]		
<i>L.a.</i> modern	32 [58–11]	6 [10–3]		
<i>L. trimucronatus</i>	134 [234–52]	22 [32–12]		

L.l. – *Lemmus lemmus*; *L.s.w.* – *L. sibiricus western lineage*; *L.s.e.* – *L. sibiricus eastern lineage*; *L.a.* – *L. amurensis*. * – node used as a calibration point

events of late Gelasian disconnected the Beringian land bridge and could have given rise to the split (Abramson and Petrova 2018) between the Eurasian *Lemmus ex gr. sibiricus-amurensis* and the East Beringian *L. trimucronatus*.

Ho et al. (2005) showed that the estimation of mutation rate depends on the time interval considered – the longer the interval, the lower the rate. So, the ages of deep nodes are underestimated when only tip dates are used for calibration. To overcome this methodological issue, we decided to use time estimates for relatively recent divergences (Late Pleistocene) obtained only with aDNA calibration. At the same time, we estimate the divergence of deep nodes using both, tip dating and the root calibration (the split of *L. trimucronatus* from the other true lemmings). Taking the paleontological data into account, we used an age of 2 Mya as a calibration point for the divergence node between the Palearctic and Nearctic lineages of the genus, although we fully

recognize the tentative and uncertain nature of such dating based on fossil remains.

Analysis of complete mitogenomes, including fossil material from newly sampled regions, confirmed the divergence of Palearctic true lemmings into two well-supported lineages, western and eastern, a pattern consistently demonstrated in a series of previous *cytb*-based studies (Fedorov et al. 1999; Abramson et al. 2008; Abramson and Petrova 2018). The substantial increase in sampling density allowed a more detailed reconstruction of the evolutionary history of the genus and population dynamics in the context of Late Pleistocene and Holocene climatic fluctuations. According to the BEAST analysis with the root calibration used (Fig. 3a; Table 2) the divergence between the western and eastern major lineages within Palearctic true lemmings was estimated as 519 kya (95% HPD 820–255 kya) after the Early-Middle Pleistocene Transition (Hughes and Gibbard 2018; Hughes et al. 2020). This deep divergence likely arose during the Middle Pleistocene, a period characterized by extensive geographic distribution of true lemmings, as evidenced by numerous fossil remains across the Palearctic (Terzea 1972; Sher et al. 1977; Janossy 1986). The lineage split may be associated with the extended glacial conditions of Marine Isotope Stage (MIS) 16. During MIS 16 the presence of a large ice sheet over the Atlantic region may have caused significant genetic divergence in *Lemmus* populations, with surviving groups persisting in refugia during the interstadial period. During the Middle Pleistocene in Eurasia, habitat fragmentation and population changes in mammals were driven primarily by climatic oscillations associated with glacial and interglacial cycles.

It is well known that Western and Eastern Eurasia have a contrast glaciation history (Sher 1991; Ehlers and Gibbard 2007; Niessen et al. 2013). While there were cover glaciations in the west, glaciers in the east were mountainous and valley-like. Paleoecological data evidence that range of the Arctic species in Europe was shifted far to the south and they survived the Pleistocene glaciations in periglacial areas (Kowalski 1995), whereas area east of the Lena River remained non-glaciated (Arkhipov et al. 1986) providing no barriers for continuous distribution of Arctic species. These differences were reflected in the patterns of genetic variability of widespread species in the western and eastern parts of their geographic ranges. Therefore, we will separately consider the evolutionary history of Palearctic lemmings in western and eastern Palearctic.

History of lemming populations in the western Palearctic

Both haplotype network and phylogenetic trees inferred from complete mitogenomes and from shorter mt fragments

(Figs. 2, 3 and 4) indicate that during the Late Pleistocene, prior to the LGM, genetic diversity was high, and lemming populations from Western Europe, the Russian Plain, and the Middle Urals were genetically connected. Several haplotypes were shared among sites from the Middle Urals and the Russian Plain (Fig. 4). By the time of the LGM, however, most haplotypes present in Western European populations and on the Russian Plain became extinct. In contrast, one *cytb* haplotype widespread in the Middle Urals during the Late Pleistocene (28.6 kya) is also characteristic of a specimen from the British Isles dated to approximately 13–12 kya, a specimen from Holocene deposits of the Northern Urals, and is widely distributed in contemporary populations of the Norwegian lemming. BEAST analysis calibrated using both root and tip dates estimates the MRCA of the western branch as ~152 kya, whereas tip-date calibration alone yields 28 kya (Fig. 3; Table 2) or 34 kya (Lord et al. 2025), just prior to the LGM. The recent estimate of the MRCA for the western clade is questionable due to the high diversity of lemmings in the Late Pleistocene. For instance, Late Pleistocene lemming specimens from Pymva Shor (Polar Urals), dated from 26 to 9.5 kya, belong to distinct clades: *L. lemmus* and *L. sibiricus* western lineage (Lord et al. 2025; supplementary materials). We therefore propose an earlier divergence of the two *Lemmus* lineages, predating the Last Interglacial. Subsequent cooling (Weichselian glaciation) beginning 114 kya (Tzedakis et al. 2013) facilitated active lemming dispersal across the European mainland, leading to high genetic diversity in the Late Pleistocene.

Thus, analysis of temporal changes in genetic diversity within the western lineage of lemmings also shows that in contrast to the collared lemming (Palkopoulou et al. 2016), haplotypes shared among different sites persist across several temporal intervals. The mt *cytb* pattern (Figs. 2 and 4) indicates evidence for only a single turnover event, likely occurring before the LGM. The obtained data support the hypothesis that the colonization of Scandinavia and the Kola Peninsula occurred after the LGM, most likely during the Late Dryas (~10 kya). During this period, the role of landscapes dominated by grass–shrub vegetation on newly deglaciated land surfaces and exposed shelf areas increased markedly around the White Sea throat (Glushankova et al. 2020). Beginning in the Atlantic period (~8 kya), rising sea levels led to the isolation of lemming populations in northern Scandinavia, the Kola Peninsula, and Novaya Zemlya. Temporal analysis of mt haplotypes clearly demonstrates the combined effects of genetic drift and bottleneck events (Fig. 4), which is further supported by the extremely low haplotype and nucleotide diversity observed in contemporary populations of the Norwegian lemming (Table 1).

Comparison of haplotype networks across three temporal layers additionally reveals a pronounced decline in genetic

diversity within the western lemming lineage from the Late Pleistocene to the present. This pattern is consistent with local extinctions of Late Pleistocene lemming populations in Central Europe and on the Russian Plain. The warming in the Holocene caused a significant shift in the habitat of the lemming's populations and a dramatic loss of mt genetic diversity. These findings support a model of extinction and genetic diminution (Stojak and Jędrzejewska 2022) in Arctic species in Europe due to climate change, revealing that only a small population of lemming recolonized post-glacial habitat while most went extinct. With the decline of European diversity stemming from climate change, modern Norwegian lemmings faced a genetic bottleneck, resulting in today's well-defined clade revealed by mitogenomes. Our findings, in conjunction with Lord et al. (2025), suggest that the divergence of this clade corresponds with deglaciation in Scandinavia, casting doubts on the previously proposed refugia hypothesis for the region (Lagerholm et al. 2014).

Notably, the expanded sampling demonstrated that, in phylogenetic reconstructions, lemming haplotypes from the southern island of the Novaya Zemlya archipelago are placed within the Norwegian lemming clade (Fig. 4, locs. 30–34), as was already noted by Spitsyn et al. (2021), whereas an individual from the northern island (Fig. 4, loc. 35) is assigned to haplogroup characteristic of the western lineage of the Siberian lemming. This archipelago is thought to be a Late Pleistocene refugium as its islands are isolated from the mainland after the LGM deglaciation, as was supposed by Spitsyn (2022). The discovery of lemmings bearing mitogenomes of *L. lemmus* on Novaya Zemlya Southern Island suggests that in the Late Pleistocene, when the archipelago was connected to the mainland, the *L. sibiricus* western lineage and *L. lemmus* represent one metapopulation with high genetic diversity. This is also evidenced by the discovery of both, Norway lemmings and Siberian lemmings (western lineage) haplotypes in the Northern Urals, Pymva Shor in the Holocene (Lord et al. 2025).

According to the results of the analyses based on *cytb* fragments of recent samples (Figs. 2 and 4), the western lineage of the Siberian lemming seems to be very compact, however, we observe some evidence of a geographical structure on the data of complete mitogenomes (Figs. 3, S4). The well-defined clade of western lineage of the Siberian lemming is clearly subdivided into two subclades, with the boundary corresponding to the Ural Mountains. Notably, the subclade comprising lemmings east of the Urals is itself further structured into distinct subclades with a conditional boundary somewhere in the central Taimyr region.

Lemming populations history in the eastern Palearctic

The exposed continental shelves in the Beringian region of Siberia are thought to have been covered by a tundra landscape and lemmings most likely persisted at this vast territory throughout the Pleistocene epoch expanding southward in cold stadials. The close genetic affinity between the Pleistocene lemming specimen from the Indigirka River region (~19 kya) and modern lemmings from Wrangel Island may be explained by the existence of a continuous tundra landscape connecting the island and the Indigirka Lowland during the LGM. Under this scenario, the present-day Wrangel Island population can be interpreted as a Pleistocene relic of this period. However, a more challenging question is raised by the fact that the nearest contemporary mainland areas to Wrangel Island (Chukotka Peninsula) are currently occupied by *L. trimucronatus*, apparently representing migrants from the North American continent, pointing to a more complex post-LGM biogeographic history of the region.

The dataset on ancient Pleistocene samples from east Siberia is significantly smaller compared to the western Eurasia, nevertheless the more striking is contrast in loss of genetic diversity over time in western and eastern parts of the genus geographic range in Palearctic. The all studied Pleistocene samples from northeastern Siberia were discovered in one region in Yakutia (Fig. 1, locs. 55, 56), and their phylogenetic placement is noteworthy. Two specimens dated to the period slightly preceding the LGM and to the LGM itself from Ogorokha River were placed within the eastern clade alongside modern *L. sibiricus* (Figs. 3 and 4), evidencing the genetic continuity over time. Only the specimen from the Tirektyakh River does not show a clear genetic affiliation with modern lemmings from this region, whereas specimens dating to the period slightly preceding the Last Glacial Maximum (LGM) and to the LGM itself, from both Yakutia and Primorsky Kray (Fig. 1, loc. 72), tend to cluster with their respective geographic clades in phylogenetic analyses. Previous work (Spitsyn et al. 2021) based on a 393 bp *cytb* fragment, obtained in Lopatin et al. (2019), has shown that the specimen from the Tirektyakh River occupies either a basal position to the entire diversity of modern Palearctic *Lemmus* or to the branch uniting *L. lemmus* and western lineage of *L. sibiricus*. Our results of *cytb* gene analysis (Fig. 2) and analyses of complete mitogenomes (Figs. 3, S4) also show indeterminate position (basal either to the eastern or to the western lineages of *Lemmus*) for this most ancient sample from east Siberia, however in all cases without a high support. It is also worth noting that, within the Late Pleistocene temporal layer, this specimen appears to show an association in the haplotype network with haplotypes of lemmings of the same age from

the Russian Plain (Fig. 4). This phylogenetic placement, considered alongside the antiquity of the specimen, could be consistent with the retention of ancestral polymorphism predating the divergence of western and eastern Eurasian true lemming lineages. Alternatively, the haplotype may represent a previously unrecognized and now extinct lineage. Distinguishing between these scenarios will require genome-wide nuclear data and expanded sampling of temporally stratified ancient material.

In general, the eastern lineage of lemmings, including both *L. sibiricus* (eastern lineage) and *L. amurensis*, demonstrates rather high genetic diversity as compared to western lineage (Table 1) indicating the stable population size in Late Pleistocene and Holocene. This is especially well pronounced if comparing the haplotype distribution at the net (Fig. 4), no star-like structures observed within the eastern lineage.

The record of *L. amurensis* from Perspektivnaya cave deserves particular attention, as it represents the southeasternmost occurrence of lemmings during the Late Pleistocene. Particularly striking is the fact that the associated small mammal assemblage from the cave deposits (where Amur lemmings' teeth were found) are taiga-associated species, that appears unexpected given the typically tundra-related ecological affinities of lemmings. Among rodents, skeletal remains of intrazonal and forest-dwelling species representatives are the most abundant in this layer (Tiunov et al. unpublished data). This faunal assemblage accumulated during MIS 2, 27–14 kya, the coldest phase of the Late Pleistocene, a period marked by pronounced and rapid shifts in vegetation structure. Palynological evidence indicates that tundra vegetation prevailed in mountainous areas, whereas lowland regions were dominated by forest–tundra and open birch–larch woodlands, with dark coniferous forests including isolated broadleaf taxa occurring only locally (Kuzmin 2004). Taken together, the coexistence of lemmings with a predominantly taiga-associated small mammal fauna under MIS 2 climatic conditions highlights the complexity of regional paleoecological conditions and suggests the presence of mosaic habitats in the southern part of the lemming range. Pronounced range fragmentation was promoted by mountain ranges and a mosaic of tundra “islands” embedded within the taiga biome. Together, these processes may have facilitated population isolation, ultimately leading to the divergence of the Amur lemming. Divergence time estimates for the Amur lemming, based exclusively on tip dating, indicate an age of approximately 60 kya (Table S2). Since then, Amur lemming populations have been isolated, and although genetic diversity analysis shows no sharp fluctuations in population size, it should be borne in mind that after the samples included in the analysis were collected, most of the species' geographic range, including its terra

typica, was flooded by the Zeya Water Reservoir, and the current status of the population is unknown.

It is remarkable that the described pattern of genetic diversity of *Lemmus* in eastern Siberia is consistent with one observed for the *Dicrostonyx* in the same region (Palkopoulou et al. 2016). Authors suggested that the higher genetic diversity of collared lemmings in the eastern part of the geographic range reflects an east-to-west dispersal and repeated recolonization of areas west of the Urals following each extinction (turnover) event. However, the data obtained for true lemmings do not support this hypothesis. The absence of star-like patterns in the haplotype network, together with the high genetic diversity observed within the eastern lineage is more consistent with long-term population stability and prolonged persistence of lemmings in eastern Siberia. There is also no evidence for east-to-west migration in this group. In contrast, patterns of haplotype variation within the western lineage indicate a postglacial expansion of lemmings from the northern Urals towards the east. This scenario is further supported by a clear eastward decline in genetic diversity, consistent with a classical leading-edge effect.

Concluding remarks

The analysis of mitogenomes of the enlarged sample of lemmings across the entire geographic range in the Palearctic, including Late Pleistocene specimens, allowed us to specify the recent evolutionary history of the genus in context of climatic oscillations over the last 50 thousand years. As expected, genetic diversity patterns in the western and eastern parts of the genus' geographic range in Palearctic differed both in space and time, reflecting the contrasting Late Pleistocene glaciation history. In accordance with expectations from this paleogeographic concept and contrary to earlier studies, enlarged sampling and mitogenome sequencing revealed significantly higher genetic diversity in non-glaciated areas than in formerly glaciated ones. Most ancient samples clustered on basal branches of the species complex, as anticipated, though some haplotypes persisted over time; this temporal variability underscores that contemporary haplogroups represent only a subset of past diversity.

Despite the strong phylogeographic structuring revealed by mitogenomes, results obtained on the mt data alone should be treated with great caution while considering species boundaries and systematics of any group. There are many examples of incongruences between mtDNA and nuclear DNA (nDNA) clustering, emphasizing uncertainties associated with drawing conclusions solely from a single non-recombining locus such as mtDNA (de Jong et al. 2023). Nonetheless, despite its well-known limitations in systematic inference, mtDNA should not be dismissed, as it can provide an unparalleled perspective on the historical

trajectory of a taxon — one that is often obscured in nuclear genomic data, which tend to primarily capture signals of more recent and contemporary population structure.

Therefore, unless the nuclear genomic data for *Lemmus* across the entire range are not analysed (will be reported elsewhere), we adhere to the conventional taxonomic division in regarding Palearctic branch of *Lemmus* as species complex of three closely related species: *L. lemmus* in Scandinavia and Kola Peninsula, *L. sibiricus* from the White Sea to Kamchatka Peninsula and *L. amurensis* in the southeastern Siberia. Without nDNA data, however, we cannot resolve deeper systematic relationships or confirm species boundaries with confidence, as mtDNA alone risks overemphasizing ancient divergences while underestimating gene flow and hybridization signals that nDNA would reveal.

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Author contributions VP: data analysis, writing - original draft preparation, writing - review and editing, TP: support with data analysis, visualisation, writing - original draft preparation, writing - review and editing. SB: data curation, support with data analysis, writing - review and editing. ID: data analysis, writing - original draft preparation, writing - review and editing. AL: data collection, writing - review and editing. NS: data collection, writing - review and editing. PAV: data collection, writing - review and editing. AK: data collection, writing - review and editing. NP: data collection, writing - review and editing. MT: data collection, writing - review and editing. NA: supervision, conceptualization, data curation, writing - original draft preparation, writing - review and editing.

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Data availability The sequences obtained in the current study were deposited in GeBank under the following accession numbers: PX867260-PX867291. Other raw data are available from the corresponding author on reasonable request.

Declarations

Ethics approval This study did not require official or institutional ethical approval.

Competing interests The authors declare no competing interests.

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