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The taxonomy and phylogeography of Palaearctic true lemmings (*Lemmus*, Cricetidae, Rodentia): New insights from cyt *b* data

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ABSTRACT. New data that significantly specified phylogeography and taxonomic structure of Palearctic lemmings (*Lemmus*) have been obtained. Therewith, the data on nucleotide composition of cyt *b* in true lemmings from the Lena River mouth, the *terra typica* for *L. sibiricus bungei* were of particular significance. It has been shown that 1) results are highly reproducible; 2) new, for the first time studied samples from the mouth of the Lena River undoubtedly referred to the west clade and thus, its border shifts to the east; 3) distinguishing of the distinct species *L. bungei* is not supported by morphological, biological, and molecular data as far as *terra typica* is inhabited by lemmings referring to the clade of typical *L. sibiricus*. New data on the variation of cyt *b* are in a good agreement with morphological, paleontological, and zoogeographical data. They better fit the taxonomic division of the genus.

KEY WORDS: *Lemmus*, phylogeography, cytochrome *b*, taxonomy.

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Таксономия и филогеография настоящих леммингов Палеарктики (*Lemmus*, Cricetidae, Rodentia): новые данные по изменчивости цитохрома *b*

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РЕЗЮМЕ. Получены новые оригинальные данные, значительно уточнившие филогеографию и таксономическую структуру палеарктических представителей рода *Lemmus.* Решающее значение, при этом, имели полученные данные секвенирования цитохрома *б* у настоящих леммингов с о-вов дельты р. Лены – *terra typica L. sibiricus bungei.* Анализ показал 1) высокую воспроизводимость результатов: наши материалы с Камчатки и с Кольского п-ова точно кластеризуются с образцами из этих регионов, изученными ранее; 2) новые, ранее неизученные образцы из дельты р. Лены вне всякого сомнения относятся к западной филогеографической кладе, и таким образом ее граница смещается на восток; 3) выделение вида *L. bungei* не только не подкреплено данными морфологии и биологии, но и молекулярными данными, так как *terra typica* заселена леммингами, без сомнения относящимися к кладе типичных *L. sibiricus*. Новые данные по изменчивости цитохрома *б* лучше согласуются как с морфологическими, палеонтологическими и зоогеографическими данными, также и с существующей таксономической схемой рода.

КЛЮЧЕВЫЕ СЛОВА: *Lemmus*, филогеография, цитохром *б*, таксономия, Палеарктика.

Introduction

The taxonomy of the genus *Lemmus* Link 1795 is not stable and was fundamentally revised several times during the 20th century. These revisions were dependant of species concepts, methods applied, and sometimes just because of an author's personal fancy to split or combine species. Three stages can be distinguished in the studies of lemming taxonomy based on the methods used. The first stage (1920s- mid 70s) of research was based on analyses of variation in fur color, body measurements, and some cranial characteristics (e.g., Vinogradov, 1925; Ognev, 1948; Krivosheev & Rossolimo, 1966). The results were controversial: the number of species varied from two to five with different number of subspecies recognized. An extreme point of view that has not received recognition was formulated by Sidorowicz (1964), who believed in the existence of a single polytypic species *L. lemmus* L., 1758 with three subspecies.

The second stage (mid 70s – end of 80s) was related to the application of cytogenetic methods and experimental hybridization (Rausch & Rausch, 1975; Pokrovskii *et al.*, 1984; Gileva *et al.*, 1984). The main and most striking result of these studies was that there were not the expected profound genetic differences between generally recognized "good species" — Norwegian (*L. lemmus*), Siberian (*L. sibiricus* Kerr, 1792), and Amur (*L. amurensis* Vinogradov, 1924) lemmings, nor between true lemmings of the New and Old World. Lemmings from the Chukotka Peninsula had a karyotype identical to North American *L. trimucronatus* Richardson, 1825, but were different from all other Eurasian lemmings (*L .lemmus*, *L. amurensis* and *L. sibiricus*, including *L. s. portenkoi* from Wrangel Island and *L. s. flavescens* from Kamchatka) in karyotype and having reproductive isolation. All the latter forms hybridized readily in experiments and have an identical karyotype (Pokrovskii *et al.*, 1984). Subsequent research had shown that there is a boundary between the two karyological forms along the Kolyma River (Fredga *et al.*, 1999). However the proposal to consider the genus as containing two species, *L. trimucronatus* and polytypic *L. lemmus* (Kuznetsova, 1995) did not receive support, and the current practice of most reviewers continues to split the genus into three (*L. lemmus*, *L. sibiricus*, and *L. amurensis* — Musser & Carleton, 1993), four (*L. lemmus*, *L. sibiricus*, *L. amurensis*, and *L. trimucronatus* — Jarell & Fredga, 1993; Gromov & Erbajeva, 1995; Pavlinov, 2006), or five separate species (Musser & Carleton, 2005: *L. portenkoi* Chernyavskii, 1967 from Wrangel Island considered as an independent species).

The novelty of the latest stage studies (i.e. through 1990s, by Chernyavskii *et al.*, 1993; Abramson, 1999a, b; Fedorov *et al.*, 1999; Fredga *et al.*, 1999) is related to the attempts to synthesize data from paleontology, paleogeography, cytogenetics, classical morphology, and finally, the analysis of mtDNA variation together with obtaining additional material from poorly surveyed regions of the Arctic. These studies have shown, in particular, that lemmings from Wrangel Island, Kamchatka Peninsula, and Amur lemmings, despite substantial differences in size and fur color, share characteristics of dentition and skull and jaw proportions with true lemmings of the Late Pleistocene (Chernyavskii *et al.*, 1993). Interestingly the relatedness of these forms was later confirmed by the analysis of nucleotide variation in the cytochrome *b* (Fedorov *et al.*, 1999). Molecular data also confirmed the previous results of cytogenetic and hybridization studies in demonstrating the large genetic divergence between *L. trimucronatus* from Chukotka and Alaska and other Eurasian true lemmings. The application of molecular – genetic data to the same material has revealed genetic separation of continental Palaearctic populations of *L. sibiricus* into western and eastern groups with the boundary putatively along the Lena River (Abramson, 1999a; Fedorov *et al.*, 1999). In this case the genetic distance was the next largest after that between *L. trimucronatius* and Eurasian true lemmings, while the level of morphological differences was low. This separation previously was not reflected in lemming taxonomy, and resurrected the subspecies *L. sibiricus bungei* Vinogradov, 1925 described from the Lena River delta which failed to receive recognition. Some authors (Fredga *et al.*, 1999; Shenbrot & Krasnov, 2005) assigned most importance to differences obtained by analyses of mtDNA and consider *L. bungei* to be a separate species, and thus distinguish five species within the genus. The morphological characteristics, however, favor its status only as a subspecies, while making inferences for taxonomy directly from quantitative evaluation of a fragment of one molecular marker is bound to a serious bias (Hendry *at al.*, 2000; Nichols, 2001; Abramson, 2007). In addition, and the most important argument against elevation of *L. bungei* to species level was that material from the Lena River delta (*terra typica* of *L. s. bungei*) was not studied. In the current paper we aimed first to analyze the lemmings from the *terra typica* of *L. s. bungei* using molecular marker cytochrom *b* and to assign it to any known lemming phylogroup (Fedorov *et al.*, 1999, 2003) and to clarify the debatable question in *Lemmus* taxonomy. Secondly we add some additional sampling to specify lemming phylogeography.

Material and methods

Samples and DNA extraction. Samples were provided by individuals or were collected during the Swedish-Russian expedition in the summer 2002 on Kola Peninsula and during Russian-German expedition “Lena delta 2001” in the summer of 2001 (Tab. 1). Total genomic DNA was extracted from ethanol preserved muscles, kidney or liver using proteinase K digestion, precipitation of proteins with phenol/chloroform and DNA precipitation with ethanol (Sambrook *et al.*, 1989).

PCR amplification and sequencing. Partial segments of cytochrome *b* (cyt *b*) gene (662 bp) were amplified by the polymerase chain reaction (PCR). The PCR included an initial 5 min denaturation step, 30 cycles of alternating denaturation at 95°C for 30 seconds, annealing at 55°C for 30 seconds, extension at 72°C for 45 seconds and a final 5 min extension step at 72°C. Specially designed pair of primers, specific for genus *Lemmus*, were used both for amplification and sequencing: 5’TCGGATCCCTCCTAGGACTT/5’GT GGATTTGCTGGGGTGTAA. Amplifications were performed in 50 μL reaction volumes with the following reagents and concentrations: primers (1 μM each), dNTP (0.2 mM), $MgCl_2$ (1.5 mM) 10x Tag buffer and *Tag* polymerase (Helicon) in a GenAmp PCR system 2700 (Applied Biosystems). All PCR experiments included negative control. PCR products were visualized on 1.5% agarose gel and then purified using Qiagen QIAquick kit. Approximately 10–30 ng of the purified PCR product was used for sequencing with each primer by autosequencing system 3730 DNA Analyzer (Applied Biosystems, Foster City, CA, USA) using ABI PRISM® BigDye™ Terminator v. 3.1. Sequences were aligned and compared manually using the Bioedit v.7.0.3 (Hall, 1999).

Data analyses. Estimates of divergence between haplotypes were calculated by using Kimura’s two parameter method, and a neighbor-joining (NJ) phylogenetic tree (Saitou & Nei, 1987). Phylogenetic and molecular evolutionary analyses were conducted using MEGA version 4 (Tamura *et al.*, 2007).

Table 1
Map references, geographical locations, abbreviations, collection numbers and GenBank Accession numbers of *Lemmus* haplotypes used in this study.

Map ref.	Geographic origin	abbreviations	N in tissue and DNA collection ZIN RAS	GenBank accession numbers	Reference
Lemmus lemmus					
1	Kola Peninsula, Ponoi	Ll1		AY219145	Fedorov et al., 2003
2	Finland	Ll1416		AF348392	Fedorov & Stenseth, 2001
3	Sweden, Vasterbotten, Ammarnas		385	FJ025984	Current study
4	Kola Peninsula, center		395	FJ025985	Current study
Lemmus sibiricus					
5	West Yamal	Ls12		AJ012671	Fedorov et al., 1999
5	West Yamal	Ls 14		AF348390	Fedorov & Stenseth, 2001
5	West Yamal	Ls2		AF348389	Fedorov et al., 2003
6	North Yamal		391	FJ025986	Current study
7	North-Western Taymyr	Ls5		AY219140	Fedorov et al., 2003
8	North-Eastern Taymyr	Ls4		AY219143	Fedorov et al., 2003
9	Olenekskiy Bay	Ls26		AJ012672	Fedorov et al., 1999
10	Lena Delta, Samoilovskii isl., terra typica *L.s.bungei*		371, 373	FJ025980 FJ025981	Current study
11	Indigirka Delta	Ls7		AJ012673	Fedorov et al., 1999
12	West bank of Kolyma	Ls6		AY219144	Fedorov et al., 2003
13	Kotelnyi Island	Ls10		AY219141	Fedorov et al., 2003
14	Fadeyevskiy Island	Ls9		AY219142	Fedorov et al., 2003
15	South-Western Wrangel Island	Ls30		AJ012677	Fedorov et al., 1999
16	Kamchatka, Uzon	Ls34		AJ012678	Fedorov et al., 1999
16	Kamchatka, Uzon		396, 399, 397	FJ025979, FJ025977, FJ025978	Current study
Lemmus trimucronatus					
17	East of Kolyma Delta	Lt2		AJ012675	Fedorov et al., 1999
18	Chukotka Peninsula, North of Anadyr		377, 378	FJ025982 FJ025983	Current study
	West Alaska*	Lt8		AJ012676	Fedorov et al., 1999
	Alaska, Goodnews Bay*	Lt22		AY219153	Fedorov et al., 2003
	Alaska, Seward Peninsula*	Lt24		AY219146	Fedorov et al., 2003
	St.George Island, Alaska*	Lt25		AY219164	Fedorov et al., 2003

* Localities in Alaska most close to the Bering Strait are not shown on the map.

Results and discussion

For the cyt *b* sequences, a total of 662 bp were scored, among which 109 sites were variable and 95 were parsimony informative. There were 28 different cyt *b* haplotypes among 28 lemmings. The neighbour-joining tree (Fig. 2) generally confirm the earlier results (Fedorov *et al*., 1999, 2003) showing the main phylogenetic division across the Kolyma River, but net divergence with addition of our material became higher – 10.5% ±1% (SE). This split in mitochondrial DNA coincides with a conventionally recognized and reproductively isolated species: Palaearctic *L. sibiricus* and Nearctic *L. trimucronatus*. Our data also confirmed the previously known second large split with a net divergence in 4.4 ± 0.9% (SE) within *L. sibiricus* proper, which conditionally divides the populations of this species into a western and eastern phylogroup. However, if

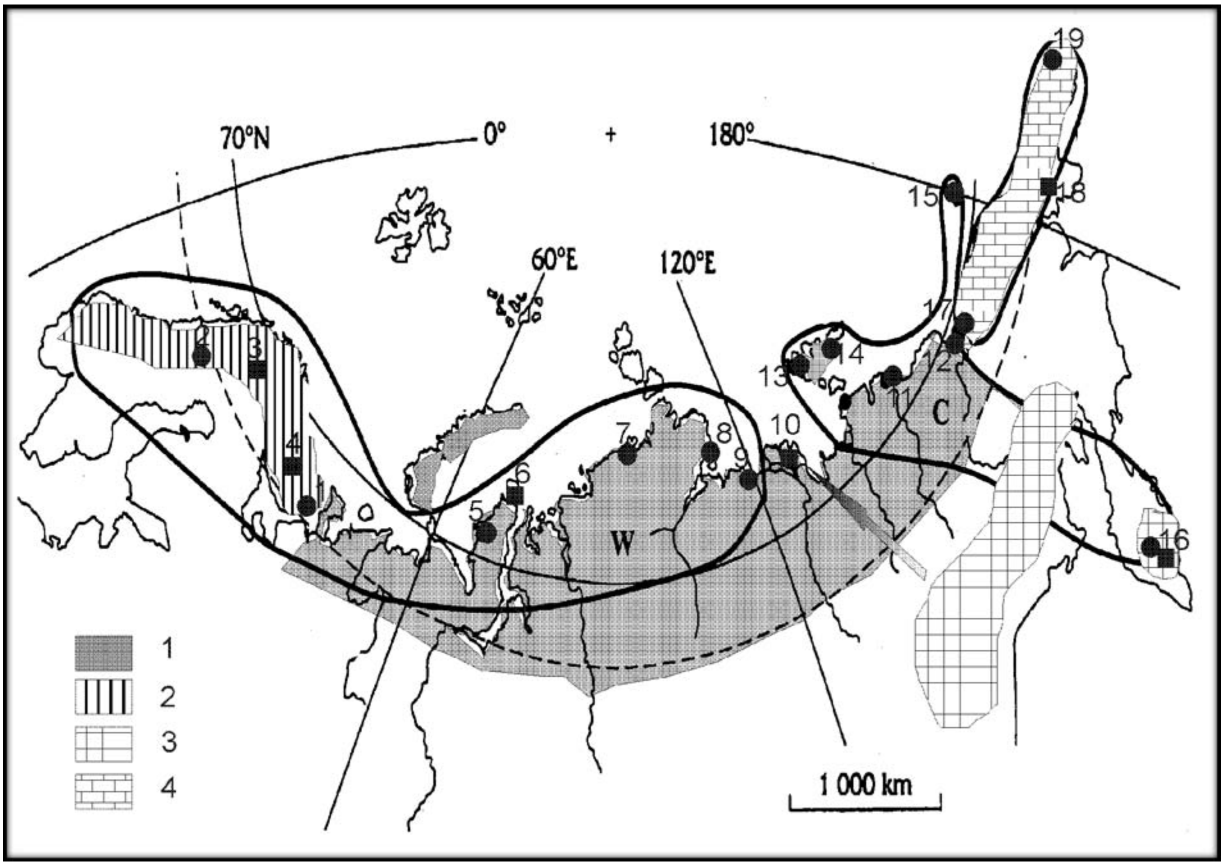

Figure 1. The map showing the recent distribution of *L. sibiricus* (1), *L. lemmus* (2), *L.amurensis* (3) and *L. trimucronatus* (4). Black circles show the geographic locations of sites from where specimens were sequenced earlier (Fedorov et al., 1999) numbers designated as in Fedorov et al., 2003 and black squares show the localities with specimens sequenced in this study (see Table 1). Black lines contour the geographic distribution of the main mtDNA clades according to Fedorov (1999), arrow point on "*terra typica*" of *L. s. bungei*.

earlier the geographical border between these phylogroups thought to be across the Lena River (Fedorov *et al*., 1999, 2003; Fredga *et al*., 1999) the results presented here clearly show that this border should be shifted to the east of Lena River delta. Our data thus finalize the debate over the species status of *L. bungei*. The specimens from the *terra typica* of this form fall within the western phylogroup forming a subclade.

The data of sequencing of samples from the mouth of the Lena River presented here excellently supported our assumption (Abramson, 1999b, 2001) and finally resolved the question on the status of the *bungei* form. While shifting the main split in cyt *b* in Palaearctic lemmings to the east of the Lena River mouth, there is no doubt that additional sampling will reveal mixed populations combining individuals of different clades, as there are no physical barriers for lemmings on this territory and they are distributed all over. So, the mitochondrial DNA splits in the given case reflect the processes of range fragmentation in the past and secondary contacts, but not the speciation process. Fossil remains of true lemmings are known from the Late Pliocene (approximately 3 Ma) and already by that time were widely distributed throughout Palaearctic (see review in Abramson, 1993). It should be underlined that proceeding from the morphological characteristics these rodents were always indicative first of all of humid environment rather than cold one, and periodical glacial advances of Pleistocene resulted in establishing on wide territory of Eurasia open landscape of the so-called tundra steppe, that was unfavorable for bog-dwelling species and best fit species more adapted to cold and dry environment. It is possible to suppose that during glacial maximums the continual range of true lemmings contracted and was fragmented into several variably isolated refugia. The following interglacial periods led to range expansion and mixing of early isolated population and resulting in high genetic variation in most recent lemming population (Ehrich & Jorde, 2005). The deep split into western and eastern groups of populations revealed in cyt *b* cladogram may reflect this past isolation when the species range was shifted far to the south and Verkhoynskii Range most probably served a natural barrier to migration. With the destruction of the tundra-steppe zone and retreat of tundra to the high latitudes true lemmings shifted their distribu-

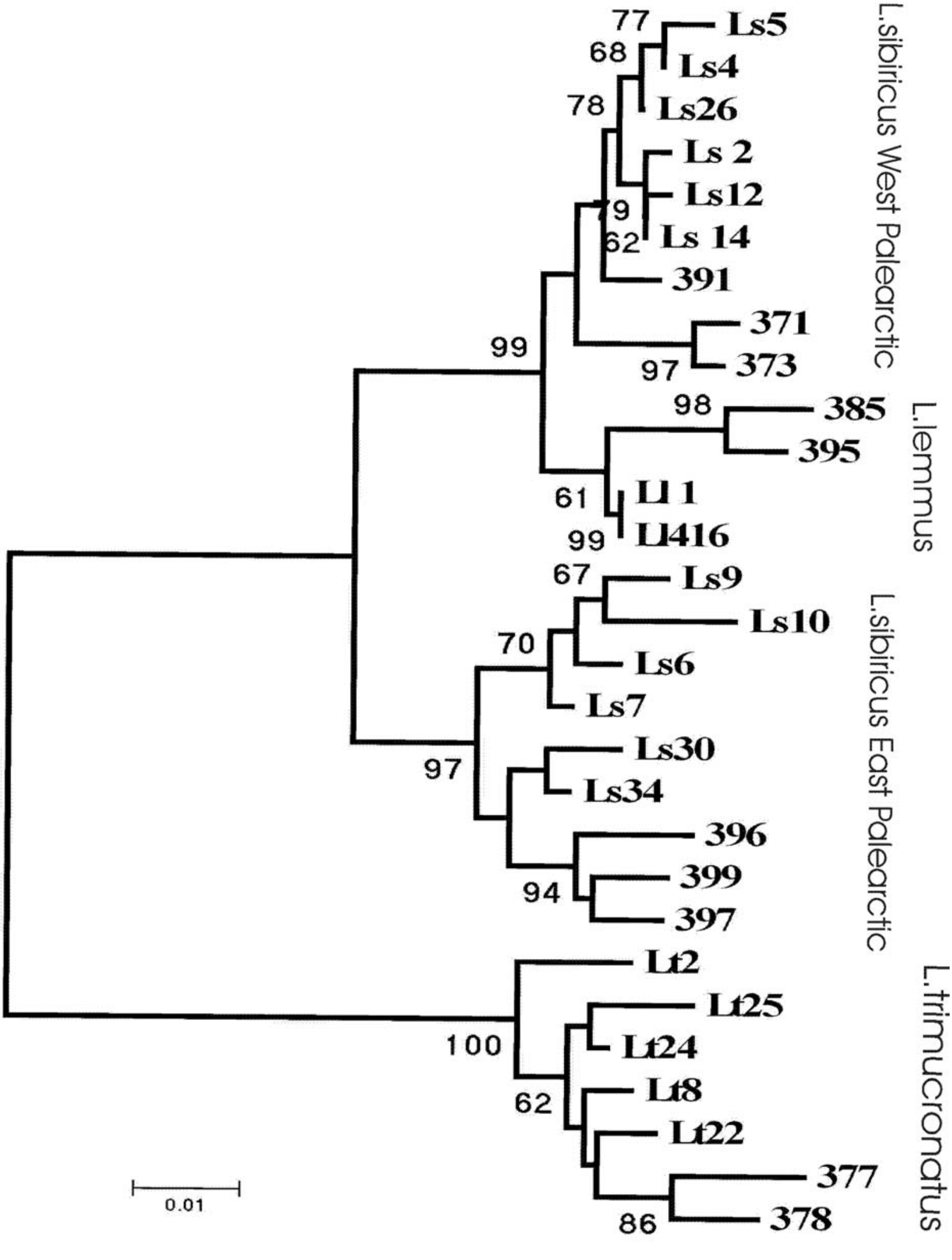

Figure 2. Neighbour-joining unrooted tree illustrating phylogenetic relationships among mtDNA haplotypes in Palaearctic *Lemmus*. The tree is based on the cyt *b* sequence divergence estimates. Geographic origin of haplotypes are given in the Table1. Numbers to the left of the node stand for a bootstrap percentage from 1000 replicates.

tion in accordance with the tundra zone and permafrost, therewith previously isolated populations appeared to be continuously distributed from the east coast of the White Sea to the west bank of the Kolyma River without any evident barrier to migration and mixing of population. Therefore, the observed deep split in mtDNA dividing lemmings into clusters of western and eastern populations does reflect events of past distribution history rather than the present day biodiversity and thus is irrelevant to the current taxonomy. However, lemmings inhabiting Fennoscandia (*Lemmus lemmus*) and those inhabiting tundra to the east of the White Sea, contrary to Siberian lemmings, are now well isolated and show definite diagnostic features in fur color, but the time of this isolation may not exceed 18000 years and quite logically we find this signature in significantly smaller genetic distance between these recognized species than between groups of continuously distributed Siberian populations. The study of nuclear molecular markers will most likely show incongruent results with mtDNA analysis. Several taxonomic decisions adequate to the up to day comprehensive knowledge of true lemmings could be adopted. If one makes choice in favor of stability of taxonomic system, what we in our turn consider to be a rather strong argument, then the current opinion recognizing four species (Jarell & Fredga, 1993; Gromov & Erbajeva, 1995; Pavlinov, 2006) will take over. The other decision which will emphasize the importance of reproductive criteria will be to distinguish only two species, *L. lemmus* and *L. trimucronatus*, while Amur and Siberian lemmings consider as subspecies (*L. l. sibiricus* and *L. l. amurensis* respectively). The most balanced decision best representing the evolutionary history of the group we see in reflecting in taxonomy the main split in true lemmings into Palaearctic and Nearctic stems by introducing the subgenus rank, and thus referring *L. trimucronatus* to one subgenus and three Palaearctic species: *L. lemmus*, *L. sibiricus, L. amurensis* to another. In our view, the optimal taxonomy of true lemmings, representing the evolutionary history of the group with the main split between Palaearctic and Nearctic lineages, would be one ranking *L. trimucronatus* and three Palaearctic species (*L. lemmus*, *L. sibiricus, L. amurensis*) as subgenera.

Alongside with always tangled and debatable taxonomy questions the example of this study rise and a number of more general issues on the possibilities and limitations of application of mitochondrial DNA markers and direct interpretations of mitochondrial DNA trees into species phylogenies and taxonomy. Molecular data and levels of divergence in the sequences of cyt *b* undoubtedly allow us to reconstruct the plausible population history, processes of range fragmentations and secondary contacts, as well as historical demography. Molecular data have a number of clear advantages over morphological data, including hardly possibly parallel origin of identical haplotypes when the nucleotide variability of the marker is high enough, environmental neutrality of considered characters, and origination of certain geographic pattern of mitochondrial haplotypes as a result of long lasting barrier to the gene flow. However, despite the obvious value of mtDNA data, it is necessary to underline that their interpretation is frequently too straightforward, and direct taxonomic conclusions are often ridiculous (Abramson, 2007).

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