

Is the Center of Origin of Long-tailed Hamster *Cricetulus longicaudatus* Milne-Edwards 1867 (Rodentia, Cricetidae) Located in Tibet?¹

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Abstract—First data on morphological and mitochondrial variation in the long-tailed hamster *Cricetulus longicaudatus* is presented. In contrast to genetically monomorphic populations of Mongolia and Tuva, the northeastern part of the Qinghai–Tibetian Plateau was found to harbor several divergent mtDNA lineages. This pattern suggests a recent expansion of the long-tailed hamster to the northern part of its recent range, which started from Tibet, presumably, in the late Middle Pleistocene. Several populations from the northern edge of the species range were found to be morphologically but not genetically distinct. The apparent disagreement between genetic and morphological data can be explained by rapid morphological evolution in peripheral isolates.

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The long-tailed hamster inhabits steppes and semi-deserts in eastern and central China, western and central Mongolia, Tuva, Trans-Baikal region, and southern Buryatia [1]. Within this range, the distribution of the species is mosaic, being associated mostly with rocky slopes and screes. The largest gap in its distribution is located in the Alashan desert and southern part of the Gobi desert.

On the basis of the morphology, several forms of the long-tailed hamster were described in the late 19th to early 20th centuries. Later, Ellerman and Morrison-Scott [2] reduced it to five subspecies: *Cricetulus l. longicaudatus* Milne-Edwards, 1867 (synonymous *andersoni* Thomas, 1908, terra typica Saratsi, Northern Shansi–Inner Mongolia, China); *C. l. griseiventris* Satunin, 1903 (Bisshengol River, south side of Altai-nuru, Gobi Altai, Mongolia); *C. l. dichrootis* Satunin, 1903 (Gorban-angyr-gol River, Nanshan, Chinese Central Asia); *C. l. nigrescens* G. Allen, 1925 (160 km

northeast of Beijing, China), *C. l. kozhantschikovi* Vinogradov, 1927 (Tukeek-kem River, Ussinsk Frontier district, Western Sayan Mountains, Siberia). Subsequently, one more subspecies of the long-tailed hamster was described from northeastern Tibet based on craniometric data [3], *C. l. chiumalaiensis* Wang et Cheng, 1973 (Chiumalai District, Sewukou Valley, Qinghai, China). In that study, the authors presented a morphology-based revision of Chinese subspecies and concluded that *C. l. dichrootis* and *C. l. nigrescens* are insufficiently distinct from the nominative subspecies and should be synonymized with it.

The long-tailed hamster is regularly included in faunistic and ecological surveys [4, 5]. However, studies focusing on this species have never been performed before, and many aspects of its interspecific variation and taxonomy are still poorly known.

Available genetic data on long-tailed hamsters are scarce [6–8]. All studies classify the long-tailed hamster as sister to the group of striped hamsters *Cricetulus barabensis* sensu lato.

In the present study, we examined long-tailed hamsters from Tuva, Buryatia, Mongolia, and China. For craniometry, we used skulls stored in the collections of the Zoological Museum of Moscow State University, Zoological Institute of Russian Academy of Sciences, American Museum of Natural History, Darwin Museum, Biogeographical Department of The Faculty of Geography of Moscow State University, St. Petersburg State University, Siberian Zoological Museum of Novosibirsk, Zoology Institute of

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Table 1. Material

	Craniometric data		<i>cyt b</i>	
	specimens	localities	specimens	localities
Tuva	26	12	6	4
Buryatia	9	3	3	1
Mongolia	80	28	31	16
China	25	8	4	4

Halle, and Zoological Museum of Berlin. The total sample includes 140 skulls from 51 localities. A detailed description of the employed methods of the craniometric analysis is given in our earlier paper [9]. Complete sequences of mitochondrial cytochrome *b* gene (*cyt b*, 1140 bp) were obtained for 44 hamsters from 25 localities (Table 1), including six sequences of *cyt b* from the GenBank (KY993920; KY993921; MG685539; MG685538; MG685540; KM067270). All new haplotypes of *cyt b* obtained in this study were deposited in the GenBank with the accession numbers MG793202–MG793226.

CRANIOMETRY

The results of the hierarchical cluster analysis of craniometric data (Fig. 1) clearly demonstrated separate positions of some of the peripheral populations (northeastern Tibet, eastern Tuva, Buryatia, and Manchuria ones) contrasting to low-variation populations of the main part of the range (southern and western Tuva, western and central Mongolia, Gobi Altai, and eastern China ones).

The most divergent morphological group includes specimens from the eastern part of the Qinghai-Tibetan Plateau, identified as *C. l. chiumalaensis*. The distance between *C. l. chiumalaensis* and other subspecies exceeds by far the difference between clearly distinct species of hamsters such as *C. sokolovi* and *C. barabensis* sensu lato [9]. Some populations from eastern Tuva are substantially differentiated from those from western and central Tuva, which group with the main cluster. Craniometric data showed that specimens from eastern Tuva are similar to the holotype *C. l. kozhantschikovi* from the western Sayan Mountains. It should be noted that specimens attributed to *C. l. chiumalaensis* and *C. l. kozhantschikovi* are significantly larger than hamsters of other subspecies; however, size correction did not eliminate this difference.

A sample from the Great Khingan Mountains, which represents a geographically isolated population, and hamsters from southern Buryatia (the Djida River valley) are also significantly differentiated from the main cluster. The high level of divergence suggests that they should be regarded as (yet undescribed) subspecies.

Within the main cluster, the largest Mahalanobis distance was observed between specimens from eastern China (including the nominative subspecies) and Mongolian samples. This can be explained by the existence of the range gap in the Alashan and southern Gobi deserts. It should be noted that, if the two subgroups are treated as separate subspecies, then the correct name for the Mongolian lineage is *C. l. griseiventris*.

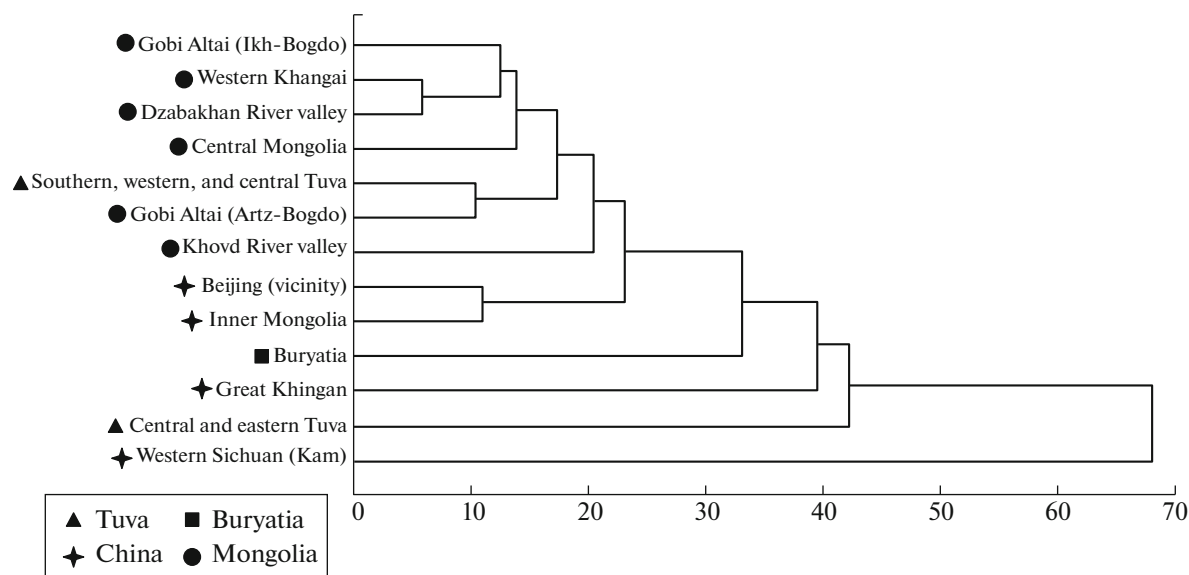


Fig. 1. An UPGMA dendrogram depicting the relationship among populations of *Cricetulus longicaudatus* based on craniometric data. The matrix of Mahalanobis distances (D^2) was used as the input.

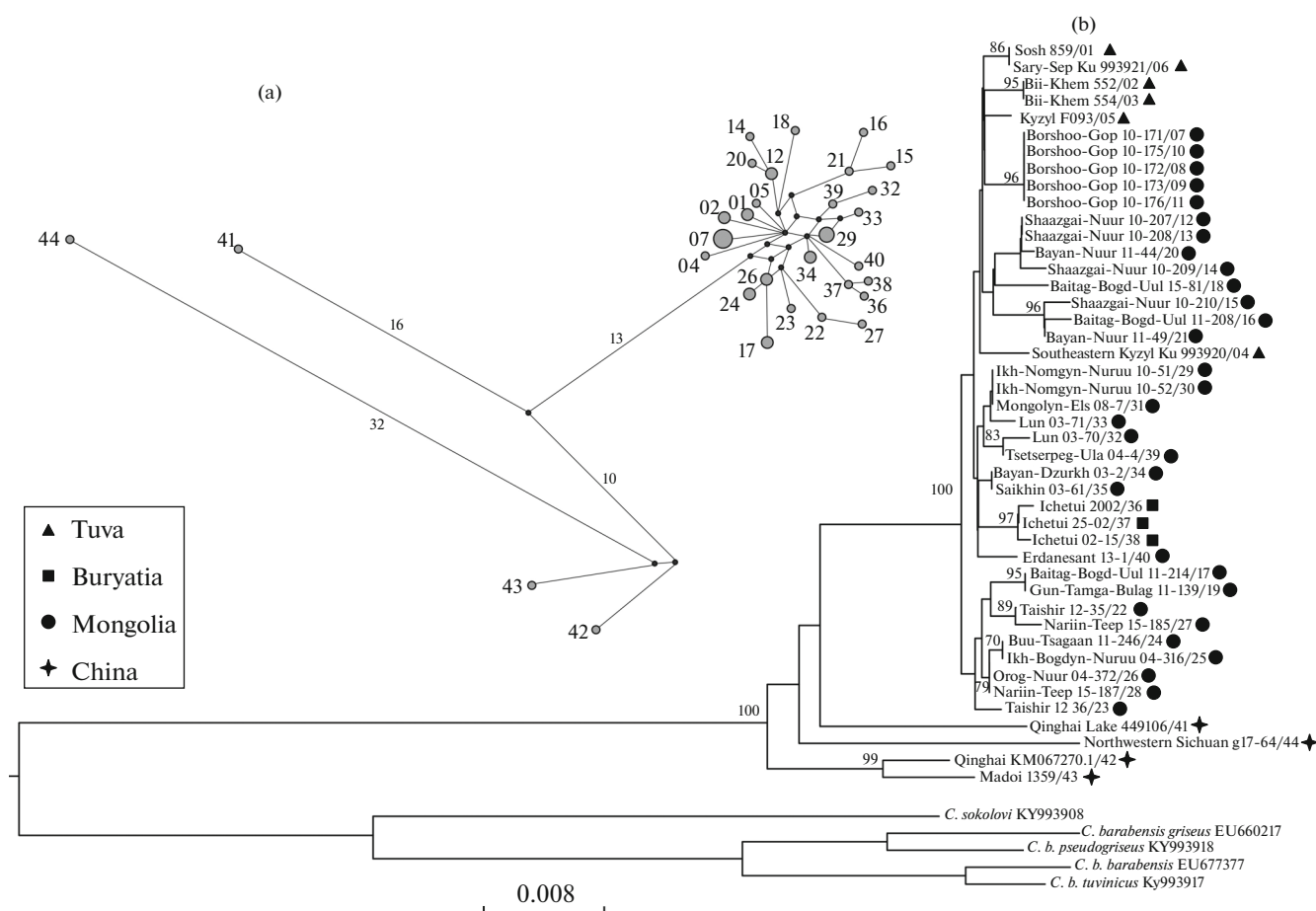


Fig. 2. The results of the analysis of the *cyt b* sequences. (a) A median-joining network of haplotypes; the number of substitutions for longer branches is shown. (b) An NJ tree reconstructed from the *p*-distance matrix, numbers at the nodes correspond to boot-strap values. OTU names include sample codes and haplotype designations as in the network.

MOLECULAR ANALYSIS

The data on range-wide genetic variation in long-tailed hamsters clearly demonstrate (Fig. 2) that most of the examined regions—Tuva, Buryatia, and Mongolia—are inhabited by hamsters belonging to the same phylogroup. In 40 specimens of hamsters from this area, 27 haplotypes were found, the mean intra-group distance (*p* distance) being 0.6%. No clear structure within this main phylogroup is evident; however, haplotypes from geographically adjacent regions tend to cluster together. At the same time, four specimens of hamsters from the northeastern part of the Qinghai–Tibetan Plateau represent three mitochondrial lineages, which are quite distant from the main phylogroup, as well as from each other. The genetic distances between the haplotypes from China and the main phylogroup were 2.7–3.3%, which is comparable to those among the three Chinese lineages (2.8–3.6%).

Mitochondrial data on the *cyt b* gene variability do not support the subdivision of long-tailed hamsters from Tuva into two groups. This can be explained either by insufficient sampling or by introgression and

fixation of alien haplotypes. The separate position of populations from Buryatia is also unsupported. Craniometric and mitochondrial data agree in showing no significant differentiation among populations of western and central Mongolia.

The data on intraspecific variation in the long-tailed hamster allow us to conclude that the primary center of diversity of the species is located in the northeastern part of the Qinghai–Tibetan Plateau. The time of divergence between the Chinese lineages and the main phylogroup was assessed using the *cyt b* substitution rate of 10.7% (as estimated for *Cricetulus barabensis* by Poplavskaya et al., unpublished data) as ca. 150 kya. Thus, the burst of radiation occurred in the end of the Middle Pleistocene; the onset of the expansion to the northern part of the range can be attributed to this time as well. The time of the most recent common ancestor of the main phylogroup is estimated as ca. 36 kya. Demographic analysis (mismatch distribution) for this sample indicates a recent demographic expansion at ca. 30 kya (supported by Tajima's *D* = −1.62, *p* = 0.03; Fu's *FS* = −12.71, *p* = 0). The time of expansion cor-

responds to the relatively warm interstadial of the Late Pleistocene. At that time long-tailed hamsters could spread widely to the north. Then, during the Last Glacial Maximum (LGM), northern populations could become isolated in separate refugia. This hypothesis corresponds to the craniometric results, which revealed separate morpho-groups in Tuva, Buryatia, and Manchuria. The discord between craniometrical and mitochondrial data can be explained by the rapid morphological evolution in peripheral populations. This conclusion is in agreement with the theory predicting higher rates of speciation in peripheral isolates [10, 11].

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