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Diversity of snow voles of the “nivalis” group (*Chionomys*, Arvicolinae, Rodentia) in the eastern part of the range with a description of a new species

Fedor N. Golenishchev*, Vladimir G. Malikov, Anna A. Bannikova, Alexander E. Zykov, Nuri Yiğit & Ercument Çolak

ABSTRACT. The genus *Chionomys* includes two supraspecific groups: “nivalis” and “gud-roberti”. For a long time, it has been thought that the nivalis group includes only *C. nivalis*. Here, molecular phylogenetic analysis of nine specimens from Turkey, Armenia, and Iran was performed using the *Cytb* gene and two nuclear genes: *BRCA1* and *GHR*. In the results on *Cytb*, two specimens from central Taurus Mountains (Turkey), morphologically similar to *C. nivalis*, stood apart from all studied *C. nivalis* geographic forms at the species level (9–12%). Meanwhile, 38 km southwest from our collection site, there is known *C. nivalis* of the Caucasian–Asia Minor molecular-genetic clade. Hence, the form from central Taurus and common Asia Minor *C. nivalis* seem sympatric. Therefore, they are most likely genetically isolated from each other as separate species. A morphometric comparison of the Taurus specimens and *C. nivalis* from the eastern part of the geographic range was carried out by principal component analysis of 12 craniometric characteristics. In some craniometric characteristics, the type specimens of the new species are clearly larger than all subspecies of *C. nivalis* from the eastern part of the range, except *C. n. layi*. That is why we consider those two central-Taurus specimens a holotype and paratype of a new cryptic species: *C. stekolnikovi* sp. nov. In addition to the morphological diagnosis, we used data on amino acid substitutions in *Cytb* and nucleotide substitutions in *BRCA1* and *GHR*.

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Разнообразие снежных полевок группы “nivalis” (*Chionomys*, Arvicolinae, Rodentia) в восточной части ареала с описанием нового вида

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РЕЗЮМЕ. Род *Chionomys* включает две надвидовые группы: “nivalis” и “gud-roberti”. Долгое время считалось, что в группе “nivalis” есть только один вид *C. nivalis*. Мы провели молекулярно-филогенетический анализ девяти образцов из Турции, Армении и Ирана с использованием гена *Cytb* и двух ядерных генов: *BRCA1* и *GHR*. В результате по *Cytb* два экземпляра морфологически схожие с *C. nivalis* из центрального Тавра (Турция) оказались дифференцированными от всех его географи-

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ческих форм на видовом уровне (9–12%). При этом, всего в 38 км к юго-западу от нашей находки известна *C. nivalis*, относящаяся к кавказско-малоазийской молекулярно-генетической кладе. Таким образом, создаётся полное впечатление, что форма из центрального Тавра и малоазийская *C. nivalis* имеют зону симпатрии и, следовательно, должны быть генетически изолированными друг от друга как разные виды. С использованием метода главных компонент по 12 краниометрическим показателям был проведён сравнительный морфометрический анализ экземпляров из Тавра и *C. nivalis* из восточной части ареала. По некоторым краниометрическим признакам типовые экземпляры нового вида явственно больше всех подвидов *C. nivalis* из восточной части ареала, кроме *C. n. layi*. Именно поэтому мы рассматриваем эти два экземпляра из центрального Тавра как голотип и паратип нового криптичсекого вида: *C. stekolnikovi* sp. nov. Помимо морфологической диагностики, мы использовали данные по аминокислотным заменам *Cytb* и нуклеотидным заменам *BRCA1* и *GHR*.

КЛЮЧЕВЫЕ СЛОВА: *Chionomys*, новый вид, цитохром *b*, *BRCA1*, *GHR*, филогенетика, морфология.

Introduction

Snow voles *Chionomys* Miller, 1908 belong to one of the basal genera within the tribe Arvicolini Gray, 1821 (Yannic *et al*., 2012; Abramson *et al*., 2021). Being rock-dwelling, they occur mostly in alpine and subalpine belts reaching a forest belt. All of them have the k-reproductive strategy (long-life, low fecundity, and late sexual maturation) (Malikov & Meyer, 1990; Hamidi *et al*., 2019). Diversity and phylogeography of snow voles of the genus *Chionomys* Miller, 1908 are a convex imprint of a specific taxon's evolution in the context of landscape-climatic history of western and southwestern Palearctic. The genus includes supraspecific groups "nivalis" and "gud-roberti". The former has traditionally been thought to be composed of a single nominative species: the European snow vole *Chionomys nivalis* (Martins, 1842) (Ellerman, 1941; Pavlinov & Rossolimo, 1987, 1998) occurring in a Glaciation Period–like environment involving a fractured rocky substrate across mountain ecosystems of Europe, the Caucasian–Asia Minor region, and a southwestern part of Asia. As a result of Pleistocene landscape-climatic shifts, a number of repeated fragmentation events and subsequent restoration events happened to the nivalis group's continuous geographic range. Within-genus diversity of *Chionomys*, especially of the nivalis group, attracted our attention owing to the evolutionary and taxonomic issues related to an extremely mosaic distribution of populations separated by considerable spatial distances. Nine subspecies of *C. nivalis* have been phenotypically distinguished across the eastern part of the species' range (Nadachowski, 1991, 1992). Additionally, *C. layi* (Zykov, 2004) from the Central Zagros (Zard-Kuh, Iran) has been described based on its distinct appearance and craniometric characteristics. Later, it was proved to be a subspecies of *C. nivalis* (Mahmoudi *et al*., 2017). Another morphologically distinct geographic form from Central Anatolia is known (Kryštufek & Vohralik, 2005). Nonetheless, *C. nivalis* intraspecific taxonomy based on phenotypic characteristics does not always align with the results of molecular genetic analyses (Yannic *et al*., 2012; Bannikova *et al*., 2013; Arslan *et al*., 2016; Mahmoudi *et al*., 2017).

In 2009 in Asiatic Turkey (a central part of the Taurus Mountains), Dr. A.A. Stekolnikov collected an adult female (ZIN 98639) (morphologically similar to *C. nivalis*) that appeared to be genetically distinct from all investigated geographic forms of *C. nivalis* at the species level (Bannikova *et al*., 2013). In addition, some nuclear genes were studied (Bondareva *et al*., 2021), and the whole mitochondrial genome was analyzed (Abramson *et al*., 2021).

Here, we researched all molecular-genetic and morphological data currently available about the nivalis group from the eastern part of its geographic range. The mitochondrial-genome data were analyzed across the entire geographic range of the nivalis group, whereas nuclear-genome data for the Middle East and Bulgaria only, and morphological data for Anatolia and Iran only. Our main aim was to compare the consistency of phenotypic, molecular-genetic, and taxonomic parameters of the nivalis group across the Caucasian-Asiatic part of its range.

Materials and methods

Material for morphological, morphometric and molecular analysis was collected in Turkey and Iran. We also used the collections of the Zoological Institute of the Russian Academy of Sciences, Saint Petersburg, Russia (ZIN); Zoological Museum of the Lomonosov Moscow State University, Moscow, Russia (ZMMU); Zoological Museum, National Natural History Museum, Ukrainian Academy of Sciences, Kiev, Ukraine (NNPM); Field Museum, Chicago, USA (FMNH) and in addition, we included in the morphological analysis a specimen ZIN 98639 (adult female, collected by A.A. Stekolnikov, 01.05.2009, from Turkey, Central Taurus Mts., Aladaglar Range, 3.5 km west from Karanfil Mt., 37.6084°N, 35.0044°E, altitude of 1709 m); a specimen from Museum of Ankara University MAU 7862 (adult male, collected by N. Yiğit, 10.09.2021, from Turkey, Central Taurus Mts., Aladaglar Range, 3.5 km west from Karanfil Mt., 37.6112°N, 34.9997°E, altitude of 1648 m; 523 m to north-west from type locality); a specimen ZIN 103591 (collected 24 km to the north-east from

the *C. n. layi* type locality Zard-Kuh Mts., 32.4525°N, 50.0422°E, altitude of 2863, Isfahan Province, Iran) and two specimens (ZIN 105323, ZIN 105324) born in the laboratory colony from parents captured at the same locality (Fig. 1, Appendix 1).

Molecular analysis

In our molecular phylogenetic analysis, we used five specimens from the Zard-Kuh Mts., Isfahan Province, Iran [MV021 (ZIN 103591), MV024 (ZIN 103592), MV025 (ZIN 103593), Chio1-2019 (ZIN 105323), and Chio2-2019 (ZIN 105324)]; one specimen from the vicinity of the village of Irind, western Armenia MV043 (ZIN 103594) and Chio2021-7862 (MUA 7862). Specimens Chio1-2019 (ZIN 105323) and Chio2-2019 (ZIN 105324) were born in the laboratory colony from female MV024 and male MV021 (Tab. 1). Then, we compared the results with those from our earlier study (Bannikova *et al*., 2013). We sequenced the complete mitochondrial *Cytb* gene and fragments of two nuclear genes: exon 11 of the breast cancer type 1 susceptibility protein (*BRCA1*) and exon 10 of the growth hormone receptor (*GHR*). Total DNA was extracted from ethanol-preserved muscle, liver, and ear tissue using a standard protocol of proteinase K digestion, phenol-chloroform deproteinization, and isopropanol precipitation (Sambrook *et al*., 1989). DNA amplification and sequencing were performed using the protocol described by Bannikova *et al*. (2013). Overall, 93 sequences of *Cytb*, 21 sequences of *BRCA1* and 21 sequences of *GHR* were used in the phylogenetic analysis. Most of these sequences were obtained in our earlier studies and/or retrieved from GenBank (Appendix 1).

To avoid the possibility of analysis of mito-nuclear pseudogenes in our *Cytb* phylogenetic reconstruction we amplified and sequenced our new specimen as well the specimen ZIN 98639 with the different systems of primers. As a whole, the following primers were used in different combinations: L14729, H15906arvic (Lebedev *et al*., 2007), Chi L444niv, Chi H604niv (Bannikova *et al*., 2013), L14734, H15985 (Ohdachi *et al*., 2001). As a result, the sequences obtained with different primers did not contain any stop-codons in the inappropriate sites or unexpected amino acid substitution and may be considered as authentic *Cytb* sequences. Besides, the obtained sequence of *Cytb* of the specimen ZIN 98639 was compared with those from the total mitogenome of this specimen (Abramson *et al*., 2021). As a result, these sequences appeared absolutely identical.

Phylogenetic reconstructions were performed separately for *Cytb* gene (Fig. 2) and two nuclear genes combined (Fig. 3). The size of the obtained amplicons without taking into account the length of the primers were from 894 bp to 974 bp for *BRCA1*, 731−905 bp for *GHR* and 1081−1140 bp for *Cytb*. Nuclear and mitochondrial phylogenetic trees were generated

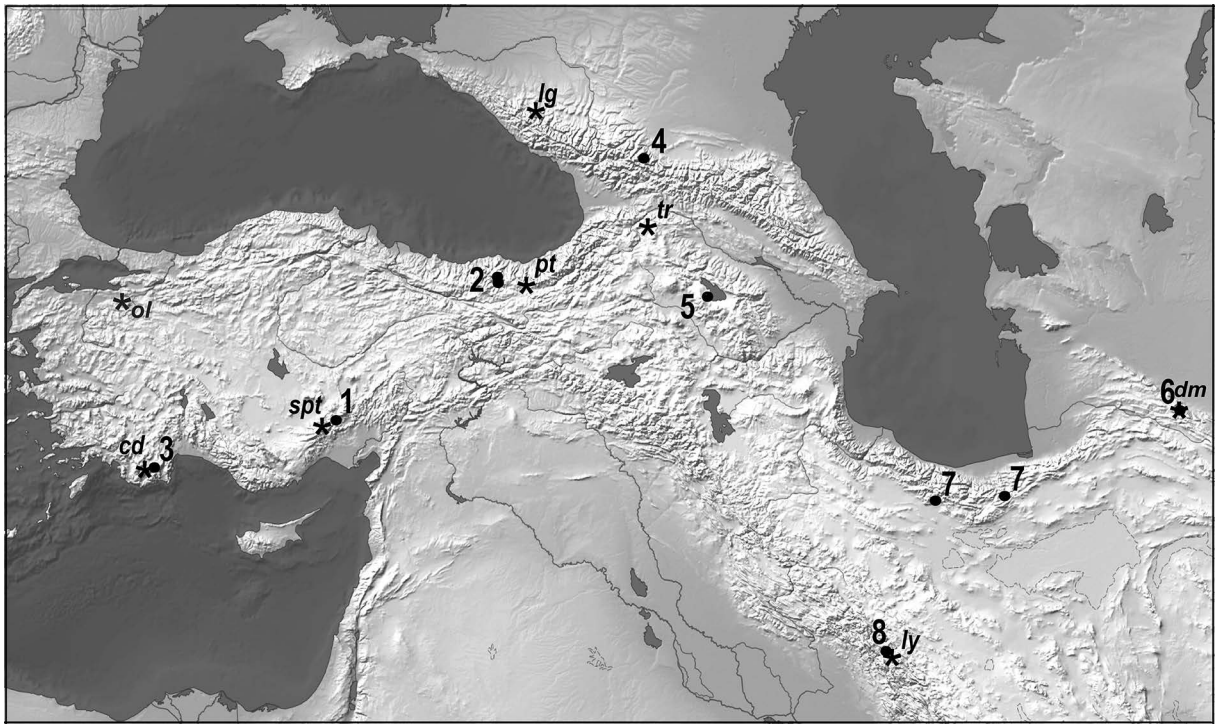

Fig. 1. Type localities of *Chionomys nivalis* subspecies from the eastern part of the range are marked with an asterisk*: *spt — spitzenbergerae, pt — pontius, cd — cedrorum, ol — olympius, lg — loginovi, tr — trialeticus, dm — dementievi, ly — C. n. layi*. Geographic localities of samples used for morphometric analysis: 1 — *C. stekolnikovi* sp. nov. ZIN 98639 and MUA 7862 (Turkey, Central Taurus, Aladaglar Range); 2 — *C. n. pontius*; 3 — *C. n. cedrorum*; 4 — *C. n. loginovi*; 5 — *C. n. trialeticus*; 6 — *C. n. dementievi*; 7 — *C. n.* ssp?; 8 — *C. n. layi*? (Iran, Zard-Kuh Mts, 24 km to north-east from *C. n. layi* type locality) (Appendix 2).

using maximum likelihood (ML) and Bayesian criteria. Maximum likelihood reconstructions were carried out in IQTree version 1.6 (Nguyen *et al*., 2015). Model Finder (Kalyaanamoorthy *et al*., 2017) was used to determine the optimum partitioning scheme and best-fit substitution models for each subset under the BIC criterion. Clade stability was tested using ultrafast bootstrap approximation (Minh *et al*., 2013) with 10 000 replicates. A Bayesian tree was reconstructed in MrBayes 3.2 (Ronquist *et al*., 2012), and separate models were assumed for each of the codon positions. The analysis included two independent runs. The chain length was set at five million generations, with sampling every 2000 generations. With these settings, the effective sample size exceeded 200 for all estimated parameters. Tracer 1.6 software (Rambaut & Drummond 2005) was used to check for convergence and determine the necessary burn-in fraction, which was 10% of the chain length. The sequences obtained in this study

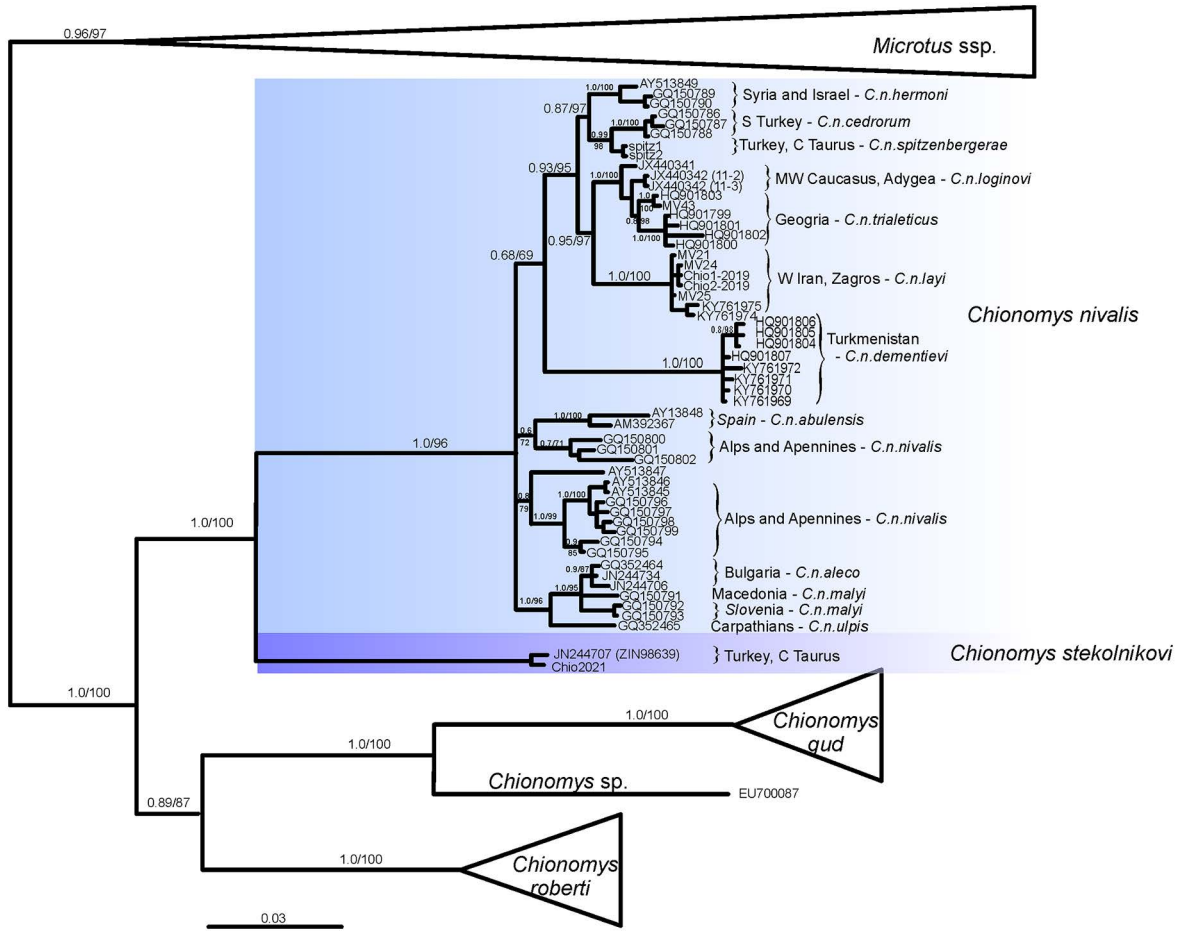

Fig. 2. Bayesian phylogeny of *Chionomys* as inferred from *Cytb* data with special attention to *C. nivalis*. Numbers before the nodes correspond to Bayesian posterior probabilities from MrBayes and ML fast bootstrap support from IQTREE (BI/ML) for the main clades, respectively.

Table 1. The original material of *Chionomys* used for the analysis of the mitochondrial *Cytb* gene and the nuclear genes *BRCA1* and *GHR*.

Species/subspecies/specimens	Coll. No.	*Cytb*	*BRCA1*	*GHR*
C. nivalis layi MV021	ZIN 103591	MT890638	MT890644	MT890648
C. n. layi MV024	ZIN 103592	MT890639	MT890645	MT890649
C. n. layi MV025	ZIN 103593	MT890640	MT890646	MT890650
C. n. layi Chio1-2019	ZIN 105523	MT890641	–	–
C. n. layi Chio2-2019	ZIN 105524	MT890642	–	–
C. n. trialeticus MV043	ZIN 103594	MT890643	MT890647	MT890651
C. stekolnikovi sp. nov.	MUA 7862	OL698789	OL698791	OL698790

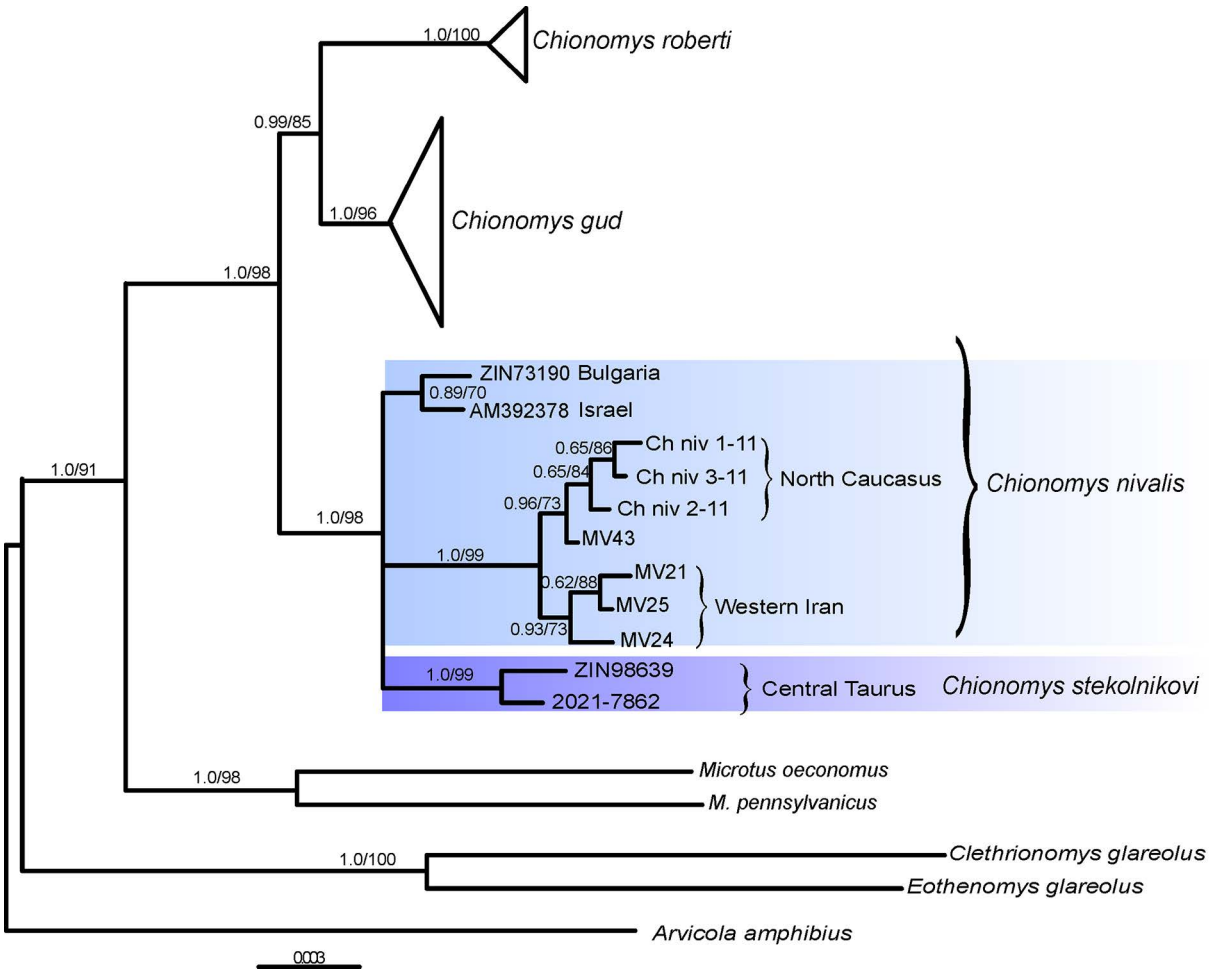

Fig. 3. Bayesian phylogenetic tree of *Chionomys* reconstructed by the concatenated *BRCA1* and *GHR* sequences. Support values are indicated similarly to Fig. 3.

can be accessed via GenBank (accession numbers: MT890638–890651 and OL698789–OL698791).

Morphometric analysis

We used out 12 measurements of 58 *C. nivalis* skulls: CBL — condylobasal length of the skull; NL — length of the nasalia; IFL — length of the incisive foramen; DL — length of the diastema; BL — length of the bullae; BB — breadth of the bullae; PBB — breadth of the palatal bridge; ZBB — breadth of the zygomatic part; BCB — breadth of the braincase; RH — height of the rostrum; BCH — height of the braincase; and M1-3 L — length of the upper teeth row.

Material measurements from ZMMU, NNPM and FMNH were performed by A.E. Zykov; ZIN and MUA — by F.N. Golenishchev. The scheme of measurements and methods of performing measurements were carefully coordinated.

Statistical analysis

Principal component analysis (PCA) was performed on 12 cranial log-transformed linear measurements using the statistical program PAST ver. 2.04 (Hammer *et al.*, 2001). Initially, with the help of this program, we made sure that there was no sexual dimorphism. The analysis was used for visual assessment of the differences between the studied *Chionomys* samples that compared within the PCA-space of particular pair of the principal components. Each sample was handly outlined by convex hull through the outmost specimens with obtaining a "sample polygon" for intergroup comparison simplification.

The sexual dimorphism effect was neglected due to (i) implementation of the logarithmic transformation of the data set and (ii) the further assessment of inter- and intragroup relations within the PCA-space.

Results

Molecular analysis — *Cytb*

The *Cytb* dataset (1140 bp) contained sequences from 57 specimens of *Chionomys* from the nivalis group and nine outgroups. The *Cytb* gene models estimated by means of IQTREE and employed in the maximum likelihood analysis were as follows: the 1st codon position: TIM2e+I+G4, the 2nd codon position: TIM3+F+I+G4, and the 3rd codon position: TIM2+F+I+G4.

The topology of the *Cytb* maximum likelihood tree of *Chionomys* (Fig. 2) was found to be mostly concordant with previously published results (Bannikova *et al*., 2013). All specimens of the nivalis group formed a strongly supported monophyletic group that was a sister taxon to the *C. gud/C. roberti* clade.

Within the nivalis group, specimens ZIN 98639 and MUA 7862 (Chio2021–7862) from Central Taurus turned out to be the most divergent. Genetic distances between these specimens and *C. nivalis* ssp. are much greater than the average intraspecific level of differentiation of snow voles (Tab. 2). Relationships among other groups of *C. nivalis* specimens could not be resolved. Our five specimens of *C. n. layi* possess the haplotype previously published for *C. n. layi* from a neighboring location in the Zagros Mountains [KY761974 and KY761975 (Mahmoudi *et al*., 2017)], with only one substitution in each of the three specimens. All specimens of *C. n. layi* clustered into a monophyletic group that was a sister taxon to the lineage of *C. n. trialeticus*+*C. n. loginovi*. Specimen MV43 from Armenia grouped with the HQ901803 sequence of *C. n. trialeticus.*

Thus, taking into account all available data, at least 12 mitochondrial lineages were distinguished within the nivalis group (if we exclude the divergent specimens from Turkey: ZIN 98639 and MUA 7862). These lineages are associated with different mountain systems and mainly correspond to recognizable morphological subspecies (Fig. 2): *C. n. hermonis* (1); *C. n. cedrorum* (2); *C. n. spitzenbergerae* (3); *C. n. trialeticus* and *C. n. loginovi* (4); *C. n. layi* (5); *C. n. dementievi* (6); *C. n. abulensis* (7); *C. n. nivalis* (two clades: 8 and 10); *C. n. mirhanreini* (9); *C. n. aleco*, *C. n. malyi*, and *C. n. wagneri* (11); and *C. n. ulpius* (12).

BRCA1 and *GHR* — In the combined analyses of these two nuclear genes, the final alignment consisted of 1879 nucleotide positions, including 974 bp of *BRCA1* and 905 bp of *GHR*. In total, the nuclear dataset contained sequences from 25 specimens, including five outgroups. The best-fit partition model for the combined analyses of *BRCA1* and *GHR*, as estimated by means of IQTREE and employed in the maximum likelihood analysis, was as follows: for the 1st and 2nd codon positions of *BRCA1* and the 2nd codon positions of *GHR*, the HKY+F+I model was utilized, whereas for the 3rd codon position of both nuclear genes and for the 1st codon position of *GHR*, the K2P model was used.

In the nuclear Bayesian tree (Fig. 3), two distinct clades are noticeable. The first clade is composed of subclades corresponding to *C. roberti* and *C. gud*. The second clade includes several distinct lineages, among them *C. n. layi* and specimens of the joint *loginovi-trialeticus* clade, whereas the specimens from Bulgaria and Israel and the specimen from the central Taurus Mountains represent independent lineages. The order of their divergence is unclear; this is because two nuclear genes are not enough to obtain a clear-cut phylogenetic signal. More loci are needed to obtain a resolved nuclear-gene tree.

The resolution of the mitochondrial-gene tree is also incomplete. With the exception of mitochondrial lineages 1–5, the position and order of divergence of the other lineages remain unclear. In particular, phylogenetic relationships of Western European lineages (*aleco*, *malyi*, *wagneri*, and *ulpius*) are uncertain. The position of *C. n. hermonis* (Israel) deep inside the radiation pattern of the Iran/Caucasus/Turkey clade in the *Cytb* tree contradicts the nuclear-gene–based reconstruction. At the same time, taking into account only moderate rather than strong support for the *aleco* + *hermonis* grouping in the nuclear tree, we believe that there is no substantial incongruence between the mitochondrial and nuclear phylogenies. Finally, mitochondrial and nuclear trees do not contradict each other regarding of the position of *C. stekolnikovi* sp. nov.

Morphometric analysis

Principal component analysis of 12 log-transformed cranial parameters resulted in the first two principal components that explained 60.92% of variance, with the first principal component (PC1) explaining 50.48% of variance and the second principal component (PC2) explaining 10.44% of variance (Fig. 4). PC1 correlated positively with length of the incisive foramen [IFL], length of the diastema [DL], and condylobasal length [CBL] (IFL, r = 0.43; DL, r = 0.43; and CBL, r = 0.33), whereas PC2 correlated positively with length of the bullae [BL], breadth of the bullae [BB], and length of the nasalia [NL] (BL, r = 0.83; BB, r = 0.39; and NL, r = 0.28). In the ordination diagram, the main group within nivalis manifested high variability of linear characteristics and a wide overlap of subspecies polygons.

Nevertheless, this group obviously separated from the type and paratype of *C. n. layi* along PC1 (Fig. 4). Moreover, cranial morphology of the specimen (ZIN 103591 "zkh 2016") from Zard-Kuh, which was collected 24 km southeast of the type locality of *C. n. layi*, does not

Table 2. Mean inter- and intraspecific (in the diagonal, are marked in italic) genetic distances (*p*-distance, %) in the genus *Chionomys.*

p-distance (%)±S.E.	*C. gud*	*C. stekolnikovi* sp. nov.	*C. nivalis*	*C. roberti*
C. gud	*3.60±0.50*			
C. stekolnikovi sp. nov.	**12.48±0.83**	*0.44±0.00*		
C. nivalis	12.14±0.79	**9.50±0.81**	*3.80*±0.30	
C. roberti	12.01±0.77	**9.83±0.78**	10.45±0.80	*0.95*±0.20

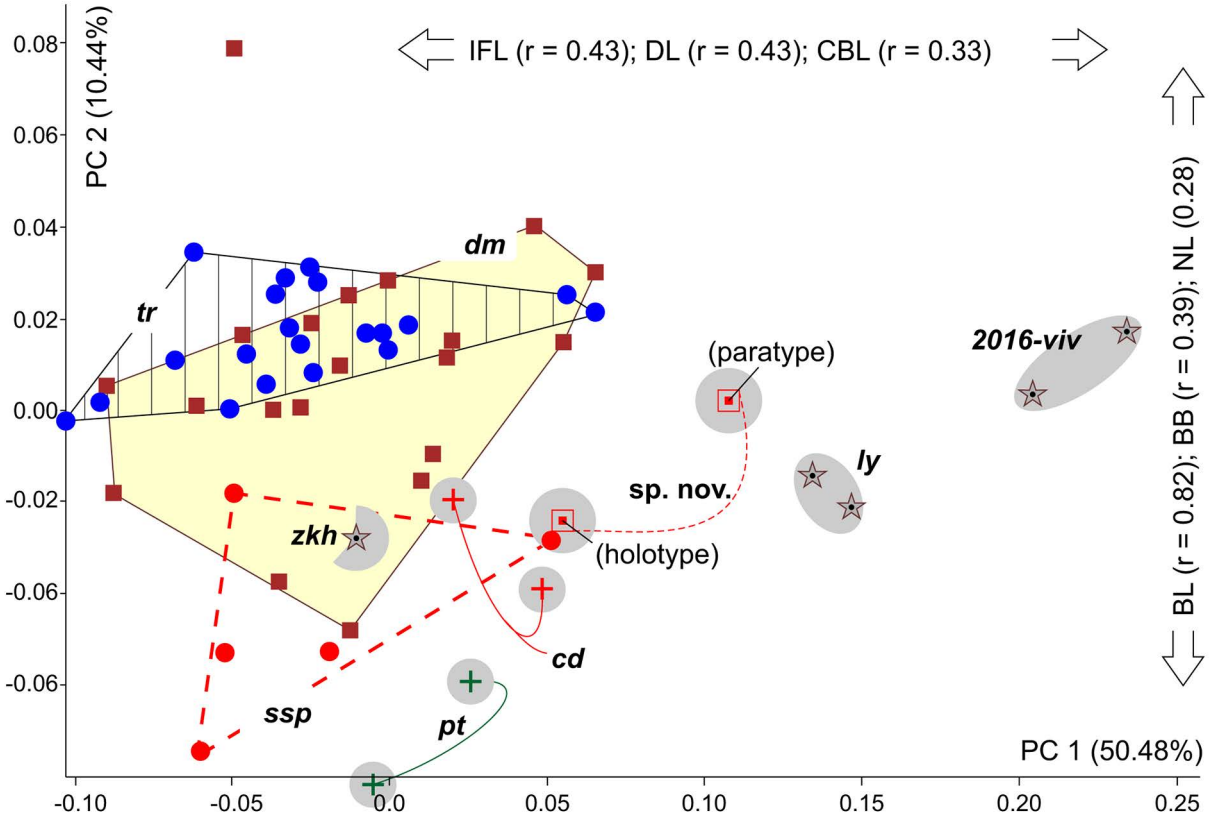

Fig. 4. Principal components plot for snow voles (the 1st axis versus the 2nd axis). Abbreviations: cd = *C. n. cedrorum*; dm = *C. n. dementievi*; ly = *C. n. layi* (h — holotype,); pt = *C. n. pontius*; ssp = unclear intraspecific form from Elburs Mts; tr = *C. n. trialeticus*; zkh = *C. layi* (ZIN 103591); "2016 viv" — *C. n. layi* (ZIN 105323, ZIN 105324 — senex, were born in the vivarium); "sp.nov." = holotype ZIN 98639, paratype MUA 7862 *C. stekolnikovi* sp. nov. Abbreviations of the measurements with values of correlation between characteristics and axis are situated at upper and right margins of the plot.

differ from cranial morphology of the main nivalis group. By contrast, the other two senile (>1 year old) specimens (ZIN 105323 and ZIN 105324 "2016") from the same site proved to be related to the same craniometric group (polygon) as are type specimens of *C. n. layi*.

Among specimens of the nivalis group, the genetically differentiated specimens ZIN 98639 and MUA 7862 from the central Taurus Mountains are closest to the type specimens of *C. n. layi* according to some absolute cranial measurements (Tab. 3). In comparison with the other forms, these two specimens, just as *C. n. layi*, showed greater condylobasal length (CBL), length of the diastema (DL), zygomatic width (ZBB), and brain chamber (BCB). In summary, the specimens of *C. n. layi* are the largest within the nivalis group according to their skull proportions (Zykov, 2004: 121).

Discussion

An integrated approach to systematics has opened up new opportunities for taxonomic interpretations of implicitly and/or ambiguously differentiated taxa. In particular, taxonomic interpretation is undoubtedly required for inconsistency between genetic differentiation and morphometric differentiation of nivalis representatives.

Chionomys n. dementievi from the Turkmenian Kopet Dag is one of examples of such inconsistency. This form is genetically distant from all the other characterized subspecies of the European snow vole (Yannic *et al*., 2012). Nevertheless, it has the same craniometrics as do the specimens obtained in the Caucasus Mountains and Asia Minor (Fig. 2). *C. n. layi* may serve as another example of the discordance between a phylogeny and phenotype. Type specimens of this subspecies differ phenotypically from all the other geographic forms of *C. nivalis*, including those from Iran (Zykov, 2004) and one specimen from Zard-Kuh (ZIN 103591, 24 km northwest from the type locality of *C. n. layi*). Nonetheless, the other two specimens from Zard-Kuh, aged at least 1 year, were found to be affiliated with the craniometric group of the type specimens of *C. n. layi* (Fig. 4).

Meanwhile, according to our work, all specimens of the nominal form belong to the molecular genetic clade that includes the Caucasian–Asia Minor specimens of *C. nivalis* (Mahmoudi *et al*., 2017, and the present study) (Figs. 2 and 3). At the same time, the *Cytb* gene analysis showed that the two central-Taurus specimens resembling *C. nivalis* are distinct from all the other geographical forms of *C. nivalis*, comparably to the distance between *C. gud* and *C. roberti*. In another words, *Cytb* gene distances

Table 3. Cranial measurements of the main forms of *Chionomys nivalis*, m±SE (min–max).

	C. stekolnikovi sp. nov. (*n*=2)	*C. n. trialeticus* (*n*=20)	*C. n. dementievi* (*n*=21)	*C. n. pontius* (*n*=2)	*C. n. cedrorum* (*n*=2)	*C. n.* ssp? Elburs (*n*=5)	*C. n. layi* (holotype and paratype) (*n*=2)	*C. n. layi* (zkh2016) (*n*=1)	*C. n. layi* (2016, vivarium) (*n*=2)
CBL	29.3–30.1	26.58±0.23(25–29)	27.26±0.21(24.6–29)	28.5–28.6	29.1 (n=1)	26.9±0.46(26–28.5)	29.5–29.8	27.9	32.2–33.4
NL	8.0–7.3	7.91±0.08(7.2–8.6)	8.11±0.11(7.1–8.8)	7.3–8.1	7.1–7.9	7.6±0.32(6.9–8.5)	8.6–8.6	8.3	9.3–10
IFL	5.4–5.2	5.04±0.08(4.4–6)	5.02±0.05(4.6–5.5)	5.1–5.3	4.7–5.4	5.02±0.29(4.3–5.8)	5.9–6.1	5	6.2–6.6
DL	9.2	8.18±0.1(7.6–9.3)	8.25±0.1(7.6–9.1)	8.5–8.9	8.7–8.9	8.38±0.19(7.9–8.9)	9.5–9.6	8.2	10.2–10.4
BL	9.0–9.5	8.93±0.07(8.5–9.8)	8.74±0.14(7.6–10.2)	7.3–7.8	8.4–9.3	7.88±0.12(7.4–8.1)	8.7–8.8	8.3	9.4–9.5
BB	6.9–6.8	6.25±0.05(6–6.7)	6.31±0.07(5.6–6.8)	6.5–6.8	7.2–7.4	6.48±0.11(6.2–6.8)	7.2–7.5	6.9	7.3–7.3
PBB	4.4–4.5	4.16±0.03(4–4.5)	4.21±0.04(4–4.5)	4–4.2	3.9–4.3	4.24±0.08(4–4.5)	4.5–4.8	4.3	4.3–4.4
ZBB	16.0–17.7	15.15±0.16(14.4–16.5)	14.93±0.13(13.6–16)	16–16.3	16.5 (n=1)	14.88±0.35(14–16)	15.6–15.6	15.3	17–17.9
BCB	14.8–15.2	13.73±0.12(12.7–14.6)	13.48±0.08(12.8–14)	12.9–14	14.2–14.3	13.32±0.16(13–13.8)	14.3–15.6	13.5	14.2–14.3
RH	6.2–8.4	7.11±0.1(6.4–8.3)	7.27±0.07(6.9–8.1)	6.9–7	6.6–7.9	7.16±0.09(7–7.5)	8.1–8.5	6.5	8.4–8.4
BCH	11.5–12	10.22±0.05(10–10.7)	10.57±0.09(10–11.3)	10.2–11.4	10.4–10.9	10.74±0.10(10.5–11)	11.2–11.5	10.2	11.9–12.2
M1-3L	6.7–6.7	6.15±0.04(5.9–6.5)	6.31±0.06(6–6.9)	6.5–6.5	6.5–7	6.3±0.16(6–6.9)	6.9–7.0	6.3	7.1–7.5

between this form and other *C. nivalis* representatives is 9–12%; this result falls within the range of interspecies divergence in Mammalia according to commonly accepted criteria (Baker & Bradley, 2006). It should be noted that a comparison of the *Cytb* gene (ZIN 98639; JN244707) with the same gene from the complete mitochondrial genome (MT381934.1) of the same specimen (Abramson *et al*., 2021) yielded a 100% match. Consequently, the pseudogene effect can be ruled out. Furthermore, both nuclear genes contain diagnostic substitutions for the specimens from central Taurus. Moreover, these genetically differentiated specimens were collected at only a 38-km distance from the type locality of *C. n. spitzenbergerae*, where Arslan *et al*. (2017) discovered representatives of the Caucasian–Asia Minor molecular genetic clade of *C. nivalis*. Therefore, according to the commonly accepted genetic characteristics of relationships between sympatric populations of different species, we regard the specimens resembling *C. nivalis* in the phenotype and collected in central Taurus Mountains as an independent cryptic species of the nivalis group. On the other hand, one can assume that such a differentiated *Cytb* gene state is simply intraspecific genetic polymorphism of *C. nivalis*. Thus, the differentiation of the genus *Chionomys* with time may be described as follows: the separation of lineages *gud* and *nivalis* (represented by our new specimens from Taurus) occurred ~3.29 Mya (Abramson *et al*., 2021). In this case, in accordance with the degree of molecular differentiation, the separation of our new specimen's *Cytb* gene lineage from all other intraspecific ones occurred approximately 2 mya. Therefore, the *Cytb* lineage from Taurus and from all *C. nivalis* members may belong to a single vole species (!) that existed at least 2 Mya, and this notion seems extremely improbable. That is why we argue that this area is inhabited by two sympatric species, namely *C. n. spitzenbergerae* and *C. stekolnikovi* sp. nov. The latter appears to be truly cryptic.

Chionomys stekolnikovi sp. nov. (Figs. 5, 6)

Holotype: ZIN 98639, adult female (skull), collected by Dr. Alexander A. Stekolnikov, coll. No. 10, 1 May 2009, Turkey, Central Taurus Mts., Aladaglar Range, 3.5 km west from Karanfil Mt. (37.6084°N, 35.0044°E), 1709 m a.s.l., from the edge of a slope in a meadow with stony soil and bushes.

Paratype: MUA No. 7862, adult male (skin and skull), collected by N. Yiğit, 10 September 2021, Turkey, central Taurus Mts., Aladaglar Range, 3.5 km west from Karanfil Mt., 37.6112°N, 34.9997°E, 1648 m a.s.l. (523 m NW from type locality);

Etymology. The species is named after the collector, A.A. Stekolnikov (Laboratory of Parasitology at the ZIN RAS).

Description:

External characteristics (paratype). Dorsal fur light brown, getting lighter toward flanks. Demarcation line between flanks and ventral side. Ventral side is whitish grey. Tail is bicolored, dorsally light brown, ventrally whitish grey. Soles of fore and hind limbs are naked, dorsally tiny hairy. Total body length: 187 mm, body length: 123 mm, tail length: 64 mm, hind foot length: 18 mm, ear length: 17, and weight: 37 g.

Skull and teeth (holotype and paratype). Condylobasal length of the skull (CBL): 29.3–30.1 mm, length of the nasalia (NL): 8.0–9.6, length of the diastema (DL): 9.2, length of the bullae (BL): 9.0–9.5 mm, breadth of the palatal bridge (PBB): 4.4–4.5 mm, breadth of the zygomatic part (ZBB): 16.0–17.7 mm, the height of the cranium with the auditory drum (BCH): 11.5–12.0 mm, and length of the upper teeth row (M1-3L): 6.7 mm. The first lower molar (m1) of the holotype is simple, with five isolated dentine plates, five protruding angles on the lingual side and four protruding angles on the labial side; in the paratype's m1, there are six isolated dentine plates, five protruding angles on the lingual side and five protruding angles on the labial side; the third upper molar (M3) of the type specimens is simple, with three labial and three lingual protruding corners and an elongated posterior lobe. The m1 anterior loop (cap) is wide in the holotype, especially in the paratype.

Diagnosis: In contrast to various forms of *C. nivalis*, the paratype of the new species is characterized by a brownish tint of dorsal fur, a distinct border between dark dorsal and light ventral parts of the body and tail, and greater relative length of the tail (52%), with the exception of *C. n. spitzenbergerae* (55%).

Compared to other forms of *C. nivalis*, the holotype and paratype skulls have greater CBL, DL, and ZBB; larger auditory bullae; and wider BCB. Nevertheless, those specimens are similar to *C. n. spitzenbergerae* in the major skull metrics except for BCB. For instance, according to Kryštufek & Vohralík (2005), in *C. n. spitzenbergerae*, BCB is 12.8–14.6, whereas in *C. stekolnikovi* sp. nov., it is 14.8–15.2. Our two specimens were also compared to the type specimen of *C. n. spitzenbergerae* (NHMW 13271) according to Spitzenberger's data (1971) because other specimens identified by a number of authors as *C. n. spitzenbergerae* may be *C. stekolnikovi* sp. nov. owing to their probable sympatry. In the type specimens of *C. stekolnikovi* sp. nov., CBL is 29.3 and 30.1 mm, whereas in the type specimen of *C. n. spitzenbergerae*, it is 29.8 mm; ZBB is 16.0, 17.7, and 17.3 mm, respectively; and BCH is 11.5, 12.0, and 12.1 mm. Compared to type specimens of *C. n. layi*, the paratype of the new species is a bit larger, but in comparison with the senex specimens of *C. n. layi*, it is smaller.

Tooth m1, being gud-roberti–like, and M3, being nivalis-like, substantially differ from those of the *C. n. spitzenbergerae* holotype (NHMW 13271) (Nadachowski, 1990) (Fig. 6). The type specimen of the new species possesses *Allophaiomys*-like m1 [see for example *Allophaiomys* cf. *chalinei* (Alcade, Agusti & Villaita, 1981) from Huétor Tájar (Spain) (Agusti et al., 1990); Fig. 3] with five isolated dentine plates owing to a merger of T5 and T4, whereas in the *C. n. spitzenbergerae* holotype, there are six, and in most *C. nivalis* representatives, there are seven. By contrast, in the *C. stekolnikovi* sp. nov. paratype, there are six isolated dentine plates. M3 in the type specimens of *C. stekolnikovi* sp. nov. is of the "simplex" morphotype (three lingual and three labial angles), whereas the *C. n. spitzenbergerae* holotype possesses the "typical-complex" morphotype (four lingual and three+one slightly developed labial angles; Fig. 6).

Given that there are no distinct phenotypic differences between *C. stekolnikovi* sp. nov. and *C. nivalis*, our diagnosis is based mostly on molecular genetic data (Tab. 4) according to Jörger & Schrödl (2013) and Renner (2016) and is supplemented with morphological information. The data on ZIN 98639 are in GenBank: *Cytb* accession No. JN244707, *BRCA1* JN244731, *GHR* JN244718 and MUA No. 7862 data: *Cytb* OL698789, *BRCA1* OL698791, and *GHR* OL698790.

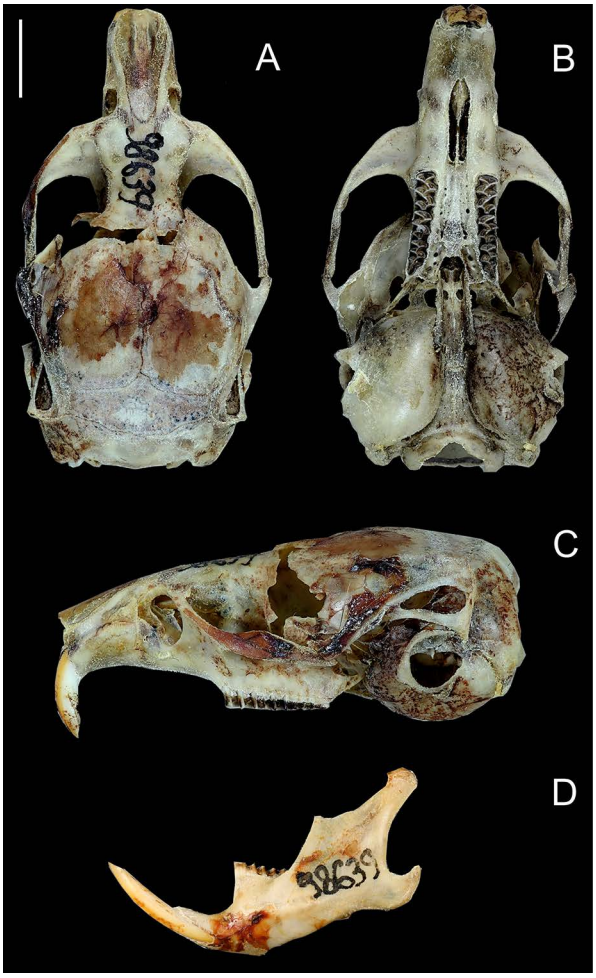

Fig. 5. The skulls of *Chionomys stekolnikovi* sp. nov. ZIN 98639. A — dorsal view; B — ventral view; C — lateral view; D — lateral view of lower jaw. Width 160 mm, scale: 1 mm.

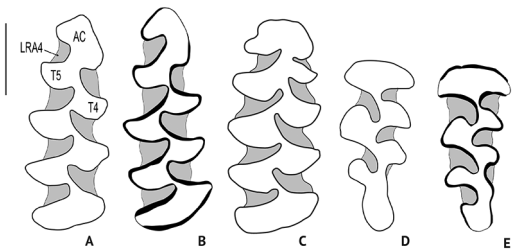

Fig. 6. The molars of holotype (A, D) and paratype (C) *Chionomys stekolnikovi* sp. nov. and holotype of *C. n. spitzenbergerae* (B, E). The first lower molar (A, B, C) and the third upper molar (D, E). Width 160 mm, scale: 1 mm.

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Table 4. Molecular diagnostic characters of *Chionomys stekolnikovi* sp. nov. Position in reference sequences correspond to amino acids for *Cytb* and nucleotides for *BRCA1* and *GHR*. The sequences of *C. nivalis*, *C. gud* and *C. roberti* are presented for comparative demonstration of diagnostic positions which are given in bold.

	Cytb		*BRCA1*	*GHR*
	amino acid		nucleotide	
positions	**42**	**295**	**75**	**72**
C. stekolnikovi sp. nov.	**V**	**V**	**g**	**t**
C. nivalis	M	I	a	c
C. gud	T	I	g, a	c
C. roberti	I	I	g, a, c	c

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Appendix 1. The GenBank sequences of *Chionomys* sp. retrieved from Genbank.

Cytb: AY513845–AY513849; GQ150786–GQ150788; GQ150791–GQ150802; KY761974, KY761975; JX440341, JX440342, JN244706, JN244707, JN244734, GQ352464, GQ352465 (*C. nivalis*); AY513850–AY513851; GQ352459, GQ352462, JX440343, JN244697–JN244705 (*C. roberti*); EU700087; JN244677–JN244691, GQ352458–GQ352461 (*C. gud*).

GHR: AM392378; JX440339, JX440340, JN244718, JN244719 (*C. nivalis*); JN244716– JN244717 (*C. roberti*); EU700087; JN244708, JN244709, JN244711– JN244714 (*C. gud*).

BRCA1: JN244731, JX440344 (*C. nivalis*); JN244728, JN244729 (*C. roberti*); JN244721–JN244724, JN244726, JN244727 (*C. gud*).

The GenBank sequences used as outgroup.

Arvicola amphibious AF119269 (*Cytb*), AM392380 (*GHR*), JX440345 (*BRCA1*); *Eothenomys melanogaster* AY426682 (*Cytb*), AM392399 (*GHR*), JX440348 (*BRCA1*); *Clethrionomys glareolus* AM392368 (*Cytb*), AM392384 (*GHR*), JX440346 (*BRCA1*); *Microtus arvalis* GQ352469 (*Cytb*); *Mynomes pennsylvanicus* AF119279 (*Cytb*), AM392376 (*GHR*), AY295009; *Agricola agrestis* AF119271 (*Cytb*); *Alexandromys oeconomus* FJ986325 (*Cytb*), AM392388 (*GHR*), JX440347 (*BRCA1*); *A. fortis* AF163894 (*Cytb*); *Lasiopodomys gregalis* GQ352466 (*Cytb*); *L. brandti* GQ352472 (*Cytb*); *Blanfordimys bucharensis* AM392369 (*Cytb*).

Appendix 2. The material of *Chionomys* used in the article.

Map ID	Voucher ID	Species/ Subspecies	Locality	Latitude	Longitude
1* **	ZIN 98639	*C. stekolnikovi* sp. nov.	Turkey, Central Taurus, Aladaglar Range, 3.5 km W from Karanfil Mt., altitude of 1709 m	37.608°N	35.004°E
1* **	MUA 7862	*C. stekolnikovi* sp. nov.	Turkey, Central Taurus Mts., Aladaglar Range, 3.5 km W from Karanfil Mt., altitude of 1648 m	37.611°N	35°E
2	ZIN 83451	*C. n. pontius*	Turkey, Mescit Ridge	40.523°N	39.442°E
2	ZIN 83449	*C. n. pontius*	Turkey, Trabzon, Zigana Ridge	40.646°N	39.404°E
3	ZIN 98637	*C. n. cedrorum*	Turkey, Beydaglar Range, Western Taurus, altitude of 2135 m	36.581°N	30.055°E
3	ZIN 98638	*C. n. cedrorum*	Turkey, Beydaglar Range, Western Taurus, altitude of 2135 m	36.581°N	30.055°E
4	ZMMU S-35124	*C. n. loginovi*	N. Caucasus, Kabardino-Balkaria	43.05°N	43.417°E
5	ZMMU S-7500	*C. n. trialeticus*	Armenia, vicinity Sevan Lake	40.233°N	45.167°E
5	ZMMU S-7501	*C. n. trialeticus*	Armenia, vicinity Sevan Lake	40.233°N	45.167°E
5	ZMMU S-7502	*C. n. trialeticus*	Armenia, vicinity Sevan Lake	40.233°N	45.167°E
5	ZMMU S-7503	*C. n. trialeticus*	Armenia, vicinity Sevan Lake	40.233°N	45.167°E
5	ZMMU S-7504	*C. n. trialeticus*	Armenia, vicinity Sevan Lake	40.233°N	45.167°E
5	ZMMU S-7505	*C. n. trialeticus*	Armenia, vicinity Sevan Lake	40.233°N	45.167°E
5	ZMMU S-7506	*C. n. trialeticus*	Armenia, vicinity Sevan Lake	40.233°N	45.167°E
5	ZMMU S-7507	*C. n. trialeticus*	Armenia, vicinity Sevan Lake	40.233°N	45.167°E
5	ZMMU S-7508	*C. n. trialeticus*	Armenia, vicinity Sevan Lake	40.233°N	45.167°E
5	ZMMU S-7509	*C. n. trialeticus*	Armenia, vicinity Sevan Lake	40.233°N	45.167°E
5	ZMMU S-7510	*C. n. trialeticus*	Armenia, vicinity Sevan Lake	40.233°N	45.167°E

Appendix 2 (continued)

Map ID	Voucher ID	Species/ Subspecies	Locality	Latitude	Longitude
5	ZMMU S-7511	*C. n. trialeticus*	Armenia, vicinity Sevan Lake	40.233°N	45.167°E
5	ZMMU S-7512	*C. n. trialeticus*	Armenia, vicinity Sevan Lake	40.233°N	45.167°E
5	ZMMU S-7513	*C. n. trialeticus*	Armenia, vicinity Sevan Lake	40.233°N	45.167°E
5	ZMMU S-7514	*C. n. trialeticus*	Armenia, vicinity Sevan Lake	40.233°N	45.167°E
5	ZMMU S-7515	*C. n. trialeticus*	Armenia, vicinity Sevan Lake	40.233°N	45.167°E
5	ZMMU S-17811	*C. n. trialeticus*	Armenia, vicinity Sevan Lake	40.233°N	45.167°E
5	ZMMU S-17821	*C. n. trialeticus*	Armenia, vicinity Sevan Lake	40.233°N	45.167°E
5	ZMMU S-92425	*C. n. trialeticus*	Armenia, vicinity Sevan Lake	40.233°N	45.167°E
5	ZMMU S-151847	*C. n. trialeticus*	Armenia, vicinity Sevan Lake	40.233°N	45.167°E
6	NNPM 10649	*C. n. dementievi*	Turkmenistan, Kopetdag	37.833°N	58.1°E
6	NNPM 10648	*C. n. dementievi*	Turkmenistan, Kopetdag	37.833°N	58.1°E
6	NNPM 10646	*C. n. dementievi*	Turkmenistan, Kopetdag	37.833°N	58.1°E
6	NNPM 10848	*C. n. dementievi*	Turkmenistan, Kopetdag	37.833°N	58.1°E
6	NNPM 11798	*C. n. dementievi*	Turkmenistan, Kopetdag	37.833°N	58.1°E
6	NNPM 11799	*C. n. dementievi*	Turkmenistan, Kopetdag	37.833°N	58.1°E
6	NNPM 11800	*C. n. dementievi*	Turkmenistan, Kopetdag	37.833°N	58.1°E
6	NNPM 11801	*C. n. dementievi*	Turkmenistan, Kopetdag	37.833°N	58.1°E
6	ZIN 29761	*C. n. dementievi*	Turkmenistan, Kopetdag, vicinity Firjuza	37.833°N	58.1°E
6	ZIN 29767	*C. n. dementievi*	Turkmenistan, Kopetdag, Shah-shah Mts.	37.817°N	58.083°E
6	ZIN 29770	*C. n. dementievi*	Turkmenistan, Kopetdag, Shah-shah Mts.	37.817°N	58.083°E
6	ZIN 29771	*C. n. dementievi*	Turkmenistan, Kopetdag, Shah-shah Mts.	37.817°N	58.083°E
6	ZIN 29772	*C. n. dementievi*	Turkmenistan, Kopetdag, Shah-shah Mts.	37.817°N	58.083°E
6	ZIN 29774	*C. n. dementievi*	Turkmenistan, Kopetdag, Shah-shah Mts.	37.817°N	58.083°E
6	ZIN 24917	*C. n. dementievi*	Turkmenistan, Kopetdag, Shah-shah Mts.	37.817°N	58.083°E
6	ZIN 24918	*C. n. dementievi*	Turkmenistan, Kopetdag, Shah-shah Mts.	37.817°N	58.083°E
6	ZIN 71277	*C. n. dementievi*	Turkmenistan, Kopetdag, Dushak Mts.	37.867°N	58.05°E
6	ZIN 71278	*C. n. dementievi*	Turkmenistan, Kopetdag, Dushak Mts.	37.867°N	58.05°E
6	ZIN 71279	*C. n. dementievi*	Turkmenistan, Kopetdag, Dushak Mts.	37.867°N	58.05°E
6	ZIN 71280	*C. n. dementievi*	Turkmenistan, Kopetdag, Dushak Mts.	37.867°N	58.05°E
6	ZIN 71283	*C. n. dementievi*	Turkmenistan, Kopetdag, Dushak Mts.	37.867°N	58.05°E
7	FMNH 97035	*C. n.* ssp.?	Iran, prov. Mazandaran, Elburs, vicinity Doab, altitude of 3047–3780 m	35.95°N	53.283°E
7	FMNH 97018	*C. n.* ssp.?	Iran, prov. Mazandaran, Elburs, vicinity Doab, altitude of 3047–3780 m	35.95°N	53.283°E
7	FMNH 97032	*C. n.* ssp.?	Iran, prov. Mazandaran, Elburs, vicinity Doab, altitude of 3047–3780 m	35.95°N	53.283°E
7	ZIN 83717	*C. n.* ssp.?	Iran, N Tehran, Elburz Mts., Darake, Palanchal, altitude of 2500 m	35.85°N	51.383°E
7	ZIN 83718	*C. n.* ssp.?	Iran, N Tehran, Elburz Mts., Darake, Palanchal, altitude of 2500 m	35.85°N	51.383°E
8*	FMNH 111842	*C. n. layi*	Iran, prov. Isfahan, Zagros, Zard-Kuh Mts., altitude of 3367 m	32.3°N	50.217°E
8	FMNH 111843	*C. n. layi*	Iran, prov. Isfahan, Zagros, Zard-Kuh Mts., altitude of 3367 m	32.3°N	50.217°E
8**	ZIN 103591	*C. n. layi* (?)	Iran, prov. Isfahan, Zagros, Zard-Kuh Mts., altitude of 2863 m	32.453°N	50.042°E
8**	ZIN 105323,	*C. layi* (?)	Iran, prov. Isfahan, Zagros, Zard-Kuh Mts., altitude of 2863 m	32.453°N	50.042°E
8**	ZIN 105324	*C. layi* (?)	Iran, prov. Isfahan, Zagros, Zard-Kuh Mts., altitude of 2863 m	32.453°N	50.042°E

* Holotypes and paratypes,
**Samples, also used in the molecular analysis.