

The first detection of a putative hybrid between Miller's and Eurasian water shrews (*Neomys milleri* and *N. fodiens*)

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ABSTRACT. We report the discovery of a water shrew specimen displaying intermediate morphological characteristics between *Neomys milleri* and *N. fodiens*, found in the Ulyanovsk region (53.8359° N, 48.4986° E). This locality is considerably distant (360–420 km) from the known range of *N. milleri*. We describe the capture location and external characteristics of the animal and present an analysis of its mitochondrial *cytb* gene and three nuclear introns (TRAIP, CSF2 and GDAP1). Although the specimen's mtDNA was initially identified as *N. milleri*, analysis of the nuclear introns revealed mixed inheritance: two were specific to *N. milleri* and one to *N. fodiens*. This combination of characteristics suggests a hybrid origin resulting from recurrent crossbreeding.

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Первая находка потенциального гибрида между малой и обыкновенной куторами (*Neomys milleri* and *N. fodiens*)

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РЕЗЮМЕ. Приведены сведения о находке в Ульяновской области (53.8359° N, 48.4986° E) экземпляра куторы с промежуточными морфологическими признаками между *Neomys milleri* и *N. fodiens*. Место находки расположено в значительном отрыве (360–420 км) от известных точек обнаружения *N. milleri*. Приведены сведения о месте поймки зверька, описаны его экстерьерные признаки, анализ последовательностей участков гена *cytb* мтДНК и трёх интронов ядерных генов (TRAIP, CSF2 и GDAP1). Данный экземпляр по последовательности мтДНК был определен как *Neomys milleri*, но имел сочетание ядерных интронов двух видов кутор, два интрона были специфичны для *N. milleri*, один – для *N. fodiens*. Подобное сочетание признаков предполагает гибридное происхождение в результате возвратных скрещиваний.

КЛЮЧЕВЫЕ СЛОВА: *Neomys*, межвидовая гибридизация, цитохром *b*, интроны, Россия.

Introduction

Interspecific hybridisation is not uncommon among Palaearctic insectivores. It has been documented in some species of the genus *Sorex* (Kunerth *et al.*, 2022; Raspopova *et al.*, 2023; Bannikova *et al.*, 2025) and *Crocidura* (Bannikova *et al.*, 2006; Dubey *et al.*, 2008; Gritsyshin *et al.*, 2023; İbiş *et al.*, 2023). It has also been observed between the species *Erinaceus euro-*

paeus and *E. roumanicus* (Bolfiková & Hulva, 2012; Curto *et al.*, 2019; Zolotareva *et al.*, 2021; Eliášová *et al.*, 2022) and is presumed to occur between *Talpa europaea* and *T. romana* (Loy *et al.*, 2001).

The genus *Neomys* currently comprises four recognised species of small, semi-aquatic mammals belonging to the family Soricidae. Two of these species have a restricted distribution: the Iberian water shrew *N. anomalous* Cabrera, 1907 is found on the Iberian Peninsula (Igea

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et al., 2015; Querejeta & Castresana, 2018), while the Transcaucasian water shrew *N. teres* Miller, 1908 is found in the Caucasus and Transcaucasia (Kryštufek & Vohralík, 2001). In contrast, the Eurasian water shrew *Neomys fodiens* (Pennant, 1771) and the Miller's water shrew *N. milleri* Mottaz, 1907 are two widespread Palearctic species. The first species, *N. fodiens*, has a wide distribution ranging from the British Isles and continental Europe to the Russian Far East and parts of Kazakhstan, Kyrgyzstan, and Mongolia (Zaitsev *et al.*, 2014; Gazzard, 2024). The second species, *N. milleri*, is sporadically distributed from Western Europe to Anatolia, encompassing Central, Southern, and Eastern Europe as far as the Middle Volga region, with isolated populations in Crimea, Turkey, Iran, and the Baltic States (Ermakov *et al.*, 2020; Gazzard & Meinig, 2023; Ermakov, 2025).

Neomys milleri is characterised by a distinct phylogeographic structure comprising two genetic lineages that differed 2.8% (*p*-distance) in the *cytb* gene. The Italian lineage is found in Italy, the Alpine region of Switzerland and north-east Spain, while the Central/Eastern lineage is found in Central and Eastern Europe and the Balkan region (Castiglia *et al.*, 2007; Igea *et al.*, 2015; Ermakov *et al.*, 2022; Neves *et al.*, 2025).

Neomys fodiens is the sister species of the other species in this genus (Kryštufek *et al.*, 2000; Castiglia *et al.*, 2007) and diverged from them approximately 1.2 million years ago (Igea *et al.*, 2015). The *cytb* differences between *N. fodiens* and *N. milleri* are very high, with a percentage of 15.3%.

The distribution ranges of *N. fodiens* and *N. milleri* overlap widely, forming a large area of sympatry. These two species can coexist in the same habitats, such as along the banks of small rivers, streams, lakes, ponds and marshes (Rychlik, 2000; Borodin, 2013). Here, we present the first documented case of a putative hybrid between Eurasian and Miller's water shrews, based on morphological and genetic data.

Material and methods

A water shrew specimen was captured in a line of three wet pitfall traps containing 10% formaldehyde between 8 August and 17 September 2023. The traps were set in the upper reaches of the Tukshumka River, a right tributary of the Volga in the Usa River basin. The capture site was located 0.7 km east of the village of Nikolskoye in the Sengileevsky district of the Ulyanovsk region, 26 km west of the Volga River bank (53.8359°N, 48.4986°E, at an altitude of 205 m). Based on its external characteristics, the specimen was provisionally identified as a Miller's water shrew. Further information is available on the "Mammals of Russia" portal (<https://rusmam.ru>) (Lukiyanov & Lobachev, 2023), as well as in a report on small mammal trapping using pitfall traps (Alpeev *et al.*, 2025).

Total genomic DNA was extracted using the formalin-fixed tissue protocol (Campos & Gilbert, 2012). For the analysis of mitochondrial DNA (mtDNA), we amplified and sequenced the *cytb* gene (1113 bp) us-

ing three overlapping primer pairs specific to *Neomys* to account for potential DNA degradation: tRNA-Glu/*cytb*_403R, *cytb*_389F/*cytb*_746R, *cytb*_614F/tRNA^{Thr} (Igea *et al.*, 2015). Four original *cytb* sequences were used from *N. milleri* specimens from the Ulyanovsk region and Mordovia (PV797253–54, this study), alongside sequences from the Penza and Tambov regions (MT855469–70, Ermakov *et al.*, 2022). Furthermore, 34 *cytb* sequences from the Central/Eastern lineage of *N. milleri* were obtained from GenBank (LK936669–70, Igea *et al.*, 2015; PQ835230–61, Neves *et al.*, 2025).

For the nuclear DNA markers, three primer pairs were used for the intron markers (TRAIP-8, 189 bp; CSF2-2, 212 bp; and GDAP1-1, 181 bp), which were previously developed for *Neomys* (Igea *et al.*, 2015) and subsequently optimised for degraded DNA (Balmori-de la Puente *et al.*, 2019). After sequencing, we determined the haplotypic phases of the introns using PHASE v. 2.1 (Stephens *et al.*, 2001) with the default settings implemented in DnaSP 6.12.03 (Rozas *et al.*, 2017). We used 18 original sequences of three intron alleles from three *N. milleri* individuals: Ulyanovsk region, Mordovia and the Tambov region (PX556876–87 and PX802687–92). We also used 110 TRAIP-8 sequences, 116 CSF2-2 sequences and 104 GDAP1-1 sequences from all four species of the genus *Neomys*, downloaded from GenBank: LK936933–952, LK936722–740 and LK936781–800 (Igea *et al.*, 2015) and LR585875–964, LR585521–614 and LR585615–698 (Balmori-de la Puente *et al.*, 2019).

We calculated mean uncorrected pairwise distances (*p*-distances) and maximum distances within the mitochondrial lineage of *N. milleri* in MEGA7 (Kumar *et al.*, 2016). We used DnaSP 6.12.03 (Rozas *et al.*, 2017) to compute the number of haplotypes (*H*), haplotype diversity (*h*) and nucleotide diversity per site (π). To infer signatures of demographic expansion, three neutrality tests were performed in DnaSP: Fu's *F_s* (Fu, 1997); *R_s* (Ramos-Onsins & Rozas, 2002); and Tajima's *D* (Tajima, 1989). Their *p*-values were calculated using 10 000 bootstrap replicates.

Haplotype networks were constructed for the *cytb* mtDNA gene of the Central/Eastern lineage of *N. milleri* and for the nuclear introns of all four *Neomys* species using the TCS algorithm (Clement *et al.*, 2002) in PopART 1.7 (Leigh & Bryant, 2015).

We conducted species distribution modelling according to the method described by Lissovsky *et al.* (2024). We used the dataset of Ermakov *et al.* (2020), together with the localities mentioned in this paper, to collect data on predictor values in places of occurrence. The background dataset was mainly collected from the European part of Russia, where sampling efforts are well documented (80% of points), and randomly across Europe (20%), to correct for differences in natural conditions between the western and eastern parts of the territory. All shrew species occurrences were used to calculate sampling efforts. The resulting raster was only used for illustration purposes.

Results

Habitat

The biotope where the putative hybrid between the Eurasian and Miller's water shrews was caught is an alder forest on the gently sloping banks of the Tukshumka River (Fig. 1). At the trap location, the river was approximately 0.5 metres deep and 1.5–2.0 metres wide. On the right bank, trees grow close to the water's edge. In contrast, the left bank has a shoreline almost devoid of woody vegetation and is 1.5–2.0 metres wide. The pitfall traps were set along the left bank, at a distance of 1.0–1.5 m from the water's edge. The soil is sandy, with muddy sediments in the upper layers. In some places, the ground was densely covered in broken or water-borne tree branches, leaves and other dead organic material, including gnawed branches left by beavers (*Castor fiber*).

The tree stand is dominated by *Alnus glutinosa*, accounting for around 90% of the stand. *Acer negundo* accounts for around 10%. The crown closure is 70–80%. Box elder is scattered throughout the understorey. The shrub layer is poorly developed. The herbaceous layer

has a projective cover of around 60%. Closer to the water's edge, the projective cover is lower (30–50%), with the area densely populated by young (juvenile, immature and virgin) specimens of *Urtica dioica*, *Epilobium roseum*, *Aegopodium podagraria*, *Impatiens noli-tangere* and *Carex* sp., reaching heights of 25–35 cm. *Cirsium oleraceum*, *Plantago major*, *Geum* sp. and *Cardamine amara* occur sporadically. Further from the water's edge and near the tree trunks, the vegetation changes, with tall stems of *U. dioica* (80 cm and higher) and *Humulus lupulus* forming dense thickets. The biotope is subject to notable anthropogenic impact; it is located 5–10 metres from a dirt road crossing the Tukshumka River at a ford and there are traces of a small herd of cattle.

The distribution model of suitable habitats confirms the edge location of the Russian population of the Miller's water shrew (Fig. 2A). The easternmost localities in the Penza region and Mordovia are situated outside the main area of distribution, in a patchy zone at the lower limit of suitability. The locality in Ulyanovsk region is situated far from suitable habitats.



Fig. 1. Habitat where the potential hybrid between Miller's and Eurasian water shrews was found (photo by Sergey Lukiyanov and Evgeniy Lobachev).

Mitochondrial marker

A total of 38 *cytb* sequences from individuals of the Central/Eastern lineage of *N. milleri*, collected from 18 sites in Poland, Slovakia, Greece, Belarus, Ukraine and Russia, were used (Fig. 2A). These included four original sequences from sites at the easternmost limits of the species' range (locs. 9–11), as well as a potential *N. fodiens* / *N. milleri* hybrid (loc. 12). The uncorrected pairwise distances for *cytb* ranged from 0% to 1.8%, with an average distance of $0.8\% \pm 0.1\%$.

The median network revealed three haplogroups (Fig. 2A). The “West” group comprised five sequences from a single location in the Sudeten Mountains, the “South” group comprised 14 sequences from five locations across the Balkans, Crimea, the Carpathians and the Central Russian Uplands, and the “North” group comprised 19 sequences from 11 locations spanning the northern part of the Eastern European Plain, from the western Carpathians to the Volga River. The mean uncorrected *p*-distances were 1.0% between the “West”/“South” and “North”/“South” comparison pairs, and 1.4% between the “West” and “North” groups. Star-like structures were observed for the “South” and “North” groups. The central haplotypes of the “North” group are from Białowieża (loc. 4), suggesting that this area was a source of dispersal for the group. Haplotypes from the eastern border localities (locs. 9–12), including a potential hybrid, form a separate branch.

The neutrality test statistics revealed significant Fu's *F_s* and Ramos-Onsins and Rozas *R₂* values for the “South” and “North” groups (see Table). Tajima's *D* values were insignificant but negative, with a *p*-value of less than 0.1. The combination of high haplotype diversity (around 0.95) and low nucleotide diversity (0.3–0.4%), together with star-shaped structures in the median network and significant negative *F_s* and *R₂* test values, suggests that the populations in the “North” and “South” groups have grown recently.

Nuclear markers

A total of 208 sequences from *N. fodiens*, 80 from *N. anomalus*, 36 from *N. milleri*, 16 from *N. teres* and six from the potential *N. fodiens* / *N. milleri* hybrid were used when considering all three introns together. Hap-

lotype genealogies based on sequences from the three introns revealed a low level of allele sharing between the three *Neomys* species (*N. anomalus*, *N. milleri* and *N. teres*), with distinct alleles observed in *N. fodiens* (Fig. 2B). The hybrid specimen contained a combination of nuclear introns from the two water shrew species, with two introns (TRAIP-8 and GDAP1-1) specific to *N. milleri* and one (CSF2-2) specific to *N. fodiens* (Fig. 2B). No heterozygous *N. fodiens* / *N. milleri* haplotypes were detected in any of the three introns of the hybrid specimen.

Discussion

In a recent study, we demonstrated that the three easternmost localities of Miller's water shrew are located in the valleys of the Tsna and Moksha rivers, which are both tributaries of the Oka River (Ermakov *et al.*, 2022). The eastern boundary of the *N. milleri* range therefore ran approximately north-south from Tambov (52.72°N, 41.52°E) through the Penza region (53.68°N, 42.20°E) to Mordovia (54.73°N, 43.17°E). The new capture site, located in the Ulyanovsk region (53.84°N, 48.50°E), is situated approximately 360–420 km east of the previously known eastern boundary of the *N. milleri* range. *Neomys fodiens* is a rare species in this area and is listed in the Red Data Book of the Ulyanovsk region as “Data Deficient” (Korol'kov, 2025).

The biotope described above corresponds to the habitat preferences of *N. milleri*. It has been found in floodplain alder forests in the eastern part of its range, including eastern Germany, Poland, northwestern Ukraine, and the Kaluga, Mordovia and Penza regions of Russia (Rychlik, 2000; Mishta, 2003; Borodin, 2013; Keckel *et al.*, 2014; Koryavchenkov, 2017; our data). Miller's water shrew prefers the ecotone between alder forest and a stream with shallow water and tufts of sedges (Rychlik, 2000). It has also been observed to be associated with large areas of shallow water formed by beaver dams (Wikar *et al.*, 2024). Conversely, the biotope in question is quite suitable for *N. fodiens*. A comparison of the preferences for macrohabitat (plant community) and microhabitat (plant cover type, distance to the stream and ground wetness) revealed interspecific overlaps of 91.4% and 90.8% respectively

Table. Genetic diversity in Miller's water shrew samples from different haplogroups.

Haplogroup	<i>n</i>	<i>H</i>	<i>h</i> ± SD	π ± SD (%)	<i>F_s</i>	<i>R₂</i>	<i>D</i>
North	19	13	0.959 ± 0.028	0.41 ± 0.04	−4.680**	0.074**	−1.438
South	14	10	0.945 ± 0.045	0.34 ± 0.05	−3.560*	0.089**	−1.361
West	5	3	0.700 ± 0.218	0.34 ± 0.01	1.775	0.231	−0.855
Central/Eastern lineage in the whole	38	26	0.979 ± 0.010	0.80 ± 0.05	−8.985**	0.067*	−1.272

n, sample size; *H*, number of haplotypes; *h*, haplotype diversity; π , nucleotide diversity (per site); *F_s*, Fu's F-statistic; *R₂*, Ramos-Onsins and Rozas *R₂*; *D*, Tajima's D test value; **p* < 0.05; ***p* < 0.01.

(Rychlik, 2000). Furthermore, when co-occurring, water shrews can develop mechanisms to reduce interference competition based on shifts in activity rhythms and maintaining distance between individuals, as well as the infrequent use of the same shelters and feeding sites (Seç *et al.*, 2023).

The morphological characteristics of the specimen under study are either typical of *N. milleri* or fall within the range of variation that overlaps between *N. milleri* and *N. fodiens*. However, the specimen is notable for its maximum hind foot length (17.9 mm), which falls within the range observed for *N. fodiens*. This hind foot length is notable for the northern part of the *N. milleri* range, where values typically do not exceed 16.5–17.0 mm, with an average of 14–15 mm (Balčiauskas & Balčiauskienė, 2012; Borodin, 2013; Balčiauskas *et al.*, 2016; Savarin & Savarina, 2019; Ermakov *et al.*, 2022). Maximum hind foot dimensions (17.8–18.3 mm) have been recorded in the southern part of the *N. milleri* range, in regions including Thrace, Asia Minor, and Crimea (Kryštufek & Vohralík, 2001; Ermakov *et al.*, 2022). Interestingly, a specimen with an intermediate hind foot length (17.2 mm) between *N. fodiens* and *N. anomalus* (= *milleri*) was previously identified in Lithuania (Balčiauskas & Balčiauskienė, 2012). The authors distinguished this specimen from typical *N. anomalus* and *N. fodiens* samples, classifying it as *N. anomalus/fodiens*.

The hybrid origin of the examined specimen is indicated by the combination of morphological and genetic features of the two water shrews (*Neomys milleri* and *N. fodiens*). The discovery of this specimen outside the known range of *N. milleri*, coupled with the absence of heterozygous nuclear markers, suggests traces of hybridisation and backcrossing rather than the formation of first-generation hybrids. However, alternative scenarios cannot be ruled out, such as incomplete lineage sorting due to ancestral polymorphism. Whole-genome sequencing techniques could resolve this question.

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Appendix

Numbers of points on the map (Fig. 2A), Latitude Longitude, GenBank IDs:

Haplogroup West: 1, 50.25N 16.856E, PQ835240, PQ835241, PQ835242, PQ835243, PQ835244.

Haplogroup North: 2, 48.29N 18.00E, PQ835256, PQ835257; 3, 54.70N 17.32E, PQ835232, PQ835233, PQ835238; 4, 52.70N 23.82E, PQ835230, PQ835231, PQ835248, PQ835249; 5, 55.23N 30.22E, LK936669; 6, 50.38N 30.45E, PQ835235, PQ835236; 7, 46.70N 32.63E, PQ835234; 8, 51.20N 37.64E, PQ835237, LK936670; 9, 52.72N 41.52E, MT855470; 10, 53.68N 42.20E, MT855469; 11, 54.73N 43.17E, PV797253; 12, 53.83N 48.50E, PV797254.

Haplogroup South: 13, 49.28N 22.52E, PQ835250, PQ835251, PQ835252, PQ835253, PQ835254, PQ835255; 14, 52.46N 33.86E, PQ835239; 15, 40.84N 21.16E, PQ835260, PQ835261; 16, 41.18N 23.14E, PQ835258; 17, 40.10N 22.49E, PQ835259; 18, 44.82N 34.12E, PQ835245, PQ835246, PQ835247.