

Taxonomy and distribution of the large serotines (*Eptesicus serotinus* sensu lato, Vespertilionidae, Chiroptera) in Mongolia

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ABSTRACT. The large serotine bats, previously classified as *Eptesicus serotinus*, are now commonly considered to represent two species: the west Palaearctic *E. serotinus* s. str. and the east Palaearctic *E. pachyomus*. Their combined range extends from western Europe and the Middle East to Korea and Indochina, but the geographical limits of the two species remain unclear. This is particularly true for Central Asia, where the large serotines are rare bats. Until recently, only four serotine localities were reported from Mongolia, and there was no consensus in the literature on the exact species identification of these specimens. In this study, we analyzed large serotines from Mongolia. Based on the mitochondrial ND1 and CytB gene sequence analysis, the specimens were identified as belonging to *E. serotinus*, contradicting the view that the Mongolian serotines represent *E. pachyomus*. The latter species report is likely a consequence of misconceptions regarding the northern margins of the *E. pachyomus* range. It is here suggested that the distribution range of the two species in Central Asia is determined by the extends of arid and moderately humid habitats, respectively, which borders significantly southwards of Mongolia.

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Систематика и распространение крупных кожанов (*Eptesicus serotinus* sensu lato, Vespertilionidae, Chiroptera) в Монголии

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РЕЗЮМЕ. Поздних кожанов, ранее относимых к виду *Eptesicus serotinus*, в современной литературе принято разделять на два вида: западный *E. serotinus* s. str. и восточный *E. pachyomus*. Их совокупный ареал простирается от Западной Европы до Кореи и Индокитая, однако пространственная граница в распространении двух видов не до конца ясна. В частности, это касается Центральной Азии, где находки крупных кожанов очень немногочисленны. До последнего времени были упоминания лишь о четырех находках позднего кожана на территории Монголии, и в литературе отсутствовало единое мнение о точной видовой принадлежности этих экземпляров. В данной работе мы проанализировали образцы крупных кожанов с территории Монголии. На основании анализа последовательностей митохондриальных генов ND1 и CytB, исследованные экземпляры были определены как принадлежащие к *E. serotinus*, что противоречит мнению о принадлежности монгольских кожанов к *E. pachyomus*. Последнее, по-видимому, является следствием ошибочных представлений о северной границе ареала *E. pachyomus*. Высказано предположение, что распространение двух видов в Центральной Азии определяется границей аридных и умеренно гумидных местообитаний, проходящей значительно южнее территории Монголии.

КЛЮЧЕВЫЕ СЛОВА: кожаны, Центральная Азия, распространение, ареалы, таксономия, генетика, границы видов.

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Introduction

The common serotine *Eptesicus serotinus* (Schreber, 1774) in broad understanding (e.g. sensu Simmons, 2005) is one of the most widespread bat species in the Palaearctic. It can be found from western Europe and the Middle East in the west through Central Asia to the Himalayas, eastern China, Taiwan, Korea in the east, and it also reaches tropical Asia in Thailand and Indochina (Simmons, 2005; Juste *et al.*, 2013; Artyushin *et al.*, 2018; Martinoli *et al.*, 2023). Such a wide distribution allows one to expect the presence of a genetic structure amongst the populations of *E. serotinus*; and this structure was indeed revealed (Juste *et al.*, 2013, Artyushin *et al.*, 2018). In the meantime, recent revisions demonstrated complex variation within the whole genus *Eptesicus* sensu lato and especially in its Old-World populations (Artyushin *et al.*, 2009, 2012a, b; Juste *et al.*, 2013), currently suggested to be referred to as the subgenus or even genus *Cnepheus* Kaup, 1829 (see Claudio *et al.*, 2023). Following these studies, it was reliably shown that the Iberian and Moroccan serotines represent a phylogenetically well-separated species, *E. isabellinus* (Temminck, 1840) (Ibáñez *et al.*, 2006). An extensive divergence in mtDNA between the European and Central Asian populations of serotines was shown to be result of the ancient DNA introgression from *E. nilssonii* (von Keyserling and Blasius, 1839) to *E. serotinus* in Europe (Artyushin *et al.*, 2009, 2012b). Also, the East and South Asian populations of the common serotine are currently often considered a species of its own, *E. pachyomus* (Tomes, 1857) (known as Oriental serotine; Juste *et al.*, 2013). The latter opinion has been questioned by Artyushin *et al.* (2018) based on results of the nuclear DNA analysis; nevertheless, it was widely accepted by various authors (Benda *et al.*, 2012; Ruedi *et al.*, 2018; Wilson & Mittermeyer, 2019; Tiunov *et al.*, 2023).

If the populations of *E. serotinus* sensu lato from the western Palaearctic became subjects of many studies and could be considered examined fairly good, then populations of the eastern Palaearctic still remain to be explored. *Eptesicus pachyomus*, if regarded as a separate species, is supposed to include four subspecies (Juste *et al.*, 2013; Srinivasulu *et al.*, 2019), namely *E. p. pachyomus* in India, Afghanistan, Pakistan and Myanmar, *E. p. andersoni* in Eastern and South-Eastern Asia, *E. p. horikawai* in Taiwan, and *E. p. pallens* in the north-east of the species distribution range. A possibly isolated population from southern Iran is supposed to belong to the nominotypical form (Benda *et al.*, 2012). The form *E. p. pallens* is traditionally thought to inhabit areas of northern China and the Korean peninsula (Ellerman & Morrison-Scott, 1951; Smith & Xie, 2008; Jo *et al.*, 2018). In the meantime, specimens reported from the Russian Far East turned out to be closer to *E. p. andersoni*, although the extremely limited material actually prevents one from determining their subspecies (Tiunov

et al., 2023). Following that opinion, this population was considered belonging to *E. pachyomus* based on genetic data from northern China (Juste *et al.*, 2013). However, information about genetic diversity within *E. pachyomus* is still quite poor, and there are a lot of blind spots in our understanding of which lineages occur across the vast area of north-western China and Mongolia.

In particular, currently published information about serotines of Mongolia is quite limited. In the 19th–early 20th century, representatives of the large *Eptesicus* were reported from just four localities of Central Asia (Bobrinskoj, 1929), of which three are situated in the Nei Mongol (Inner Mongolia) Province of China and only one record, made in 1880 from the vicinity of the Khurhe Mountains, is situated within Mongolian borders (Bannikov, 1954). These records were tentatively associated with *E. serotinus turcomanus* by Bobrinskoj (1929). After that, a single specimen of large *Eptesicus* was captured in Mongolia in 2005 and was supposed to belong either to the form *turcomanus* or *pallens*, based on the pelage coloration and the distribution grounds (Dolch *et al.*, 2007). Later, Datzman *et al.* (2012) considered that the Mongolian large serotines are positioned phylogenetically close to *E. s. turcomanus* based on the analysis the ND1 gene sequences. However, they avoided any final conclusions because of absence of any data on the same gene for the Oriental serotine populations. Until 2021, only four sites of the large serotines were reported from the Mongolian territory (Dolch *et al.*, 2021). These animals were considered either *E. serotinus* sensu lato (Jargalsaikhan *et al.*, 2022) or *E. pachyomus* (Dolch *et al.*, 2021; Batsaikhan *et al.*, 2022).

Thus, the subspecific or even specific affiliation of the Mongolian large serotines still requires clarification, as well as location of the distributional boundaries of *E. serotinus* and *E. pachyomus* in the north-eastern Palaearctic. In the last few years, additional data on the serotine distribution in Mongolia together with new genetic samples were obtained due to field work of the Joint Russian-Mongolian complex biological expedition of the Russian and Mongolian Academies of Sciences. Therefore, it becomes possible to bring certain suggestions to the subject mentioned above that can help to clarify the geographical and taxonomic questions concerning the occurrence of the large serotines in Asia.

Material and methods

The original material for this study consists of seven samples of the large *Eptesicus* bats, which were considered to be *E. serotinus* sensu lato when identified in the field. These bats were captured in three sites (Fig. 1, Table 1) using mist nets during the field work of the Joined Russian-Mongolian expedition in August 2024. Wing membrane biopsies were sampled using a 3 mm skin biopsy punch and preserved in 96% ethyl alcohol at –20 C until the DNA extraction. All collected tissue

samples are stored in the Zoological Museum of Moscow State University (Moscow, Russia) and in the collection of the Institute of Biology, Mongolian Academy of Science (Ulaanbaatar, Mongolia).

Table 1. Currently known localities of the serotine, *Eptesicus serotinus*, in Mongolia. Note, that no genetic data is available for the specimen from Khurhe Mountains (Bobrinskiy, 1929).

Collecting locality	Coordinates	Reference
Khurhe Mountains	N 42.41°, E 105.74°	Bobrinskiy, 1929
Bordzongijn-gobi	N 42.4833°, E 105.25°	Datzman <i>et al.</i> , 2012
Oasis Zulganai	N 43.5840°, E 100.0682° N 43.5836°, E 100.0713°	Dolch <i>et al.</i> , 2007 and this study
Gurvantes sum, Delijn us	N 42.9803°, E 100.6668°	Dolch <i>et al.</i> , 2021
Hulstai Bulag	N 42.9447°, E 101.6080°	this study
Nojon, Saryn Hyondiy	N 43.2090°, E 101.8945°	this study
Zaylan Bulag	N 42.4100°, E 102.2580°	this study

For the genetic analysis we used two mitochondrial markers — the cytochrome *b* gene (CytB) and the first subunit of NADH dehydrogenase gene (ND1), since these two genes were used in previous studies for delimitation of *E. pachyomus* and *E. serotinus* (Juste *et al.*, 2013; Artyushin *et al.*, 2018; Tiunov *et al.*, 2022). The DNA was isolated from the ethanol preserved wing membrane samples using standard phenol-chloroform extraction method (Sambrook *et al.*, 1989). We used ER65 and ER66 primers for ND1 amplification and sequencing (Mayer & von Helversen, 2001); for CytB L14108_pip and H15395_pip (Kruskop *et al.*, 2020, and Artyushin *et al.*, 2009, accordingly) were used. The standard PCR was conducted, 35 cycles of which included denaturation at 94°C for 30 seconds, annealing at 58°C for 60 seconds and elongation at 72°C for 60 seconds for both primer systems. Predenaturation lasted for 3 minutes at 94°C and the final elongation lasted for 10 minutes at 72°C. PCR-products were visualized using 1% agarose gel and then purified using Diatom[™] DNA PCR Clean-Up kit. The purified PCR-product was sequenced with the same primers used for PCR on ABI Prism 3500 (Applied Biosystems, USA).

Obtained sequences were aligned using Lasergene SeqMan Pro V7.1.0 (DNASTAR, Inc.), and then the alignments were trimmed and finalized in Bioedit

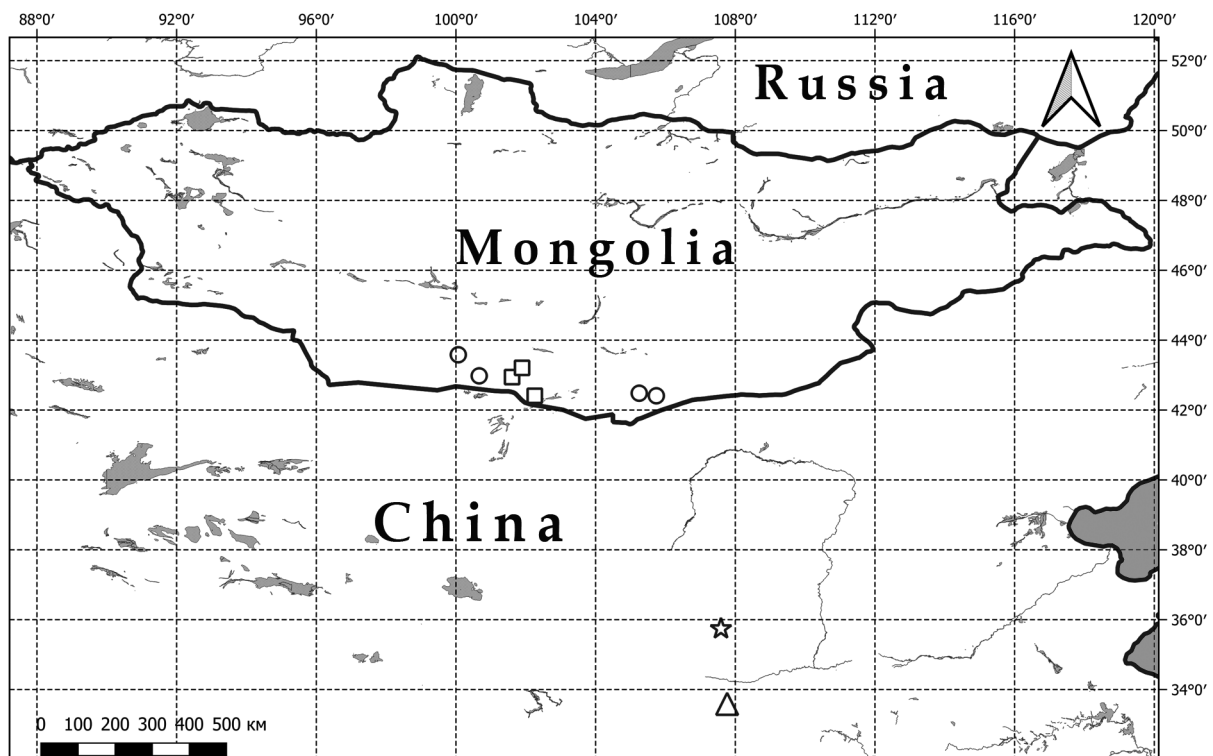


Fig. 1. Map of *E. serotinus* findings in Mongolia and the type locality of *E. pachyomus pallens*. Localities documented by the Russian-Mongolian Biological expedition are marked with squares; previously published records are marked with circles; type locality of *E. p. pallens* is marked with asterisk; locality of genetically identified *E. pachyomus* (Juste *et al.*, 2013) is marked with triangle.

V7.0.5.3 (Hall, 1999). The length of final ND1 gene alignment was 665 bp and 1140 bp for the CytB gene. For the first one a sequence of *Pipistrellus pipistrellus* was taken as an outgroup (accession number MN158283.1) and for the second one we used an *Arielulus circumdatus* sequence (PV289746.1) as an outgroup. We used MrBayes V3.2.7 (Ronquist *et al.*, 2012) for the alignment analysis and for the construction of phylogenetic trees. The best-fit models were found using IQ-Tree3 (Wong *et al.*, 2025), ModelFinder module (Kalyaanamoorthy *et al.*, 2017) and partition finder module (Chernomor *et al.*, 2016). Information regarding the best-fit models used in this study can be found in Table 2. The MCMC chain in Bayesian analysis consisted of 9 million steps for CytB and 6 million steps for ND1. The sufficient number of steps was assessed using Tracer V1.7.2 (Rambaut *et al.*, 2018). The trees were visualized using FigTree V1.4.4 (<http://tree.bio.ed.ac.uk/software/figtree/>).

Table 2. Best-fit models for CytB and ND1 genes according to IQ-Tree3 partition finder and ModelFinder modules (see text), used in Bayesian analysis in this study.

Gene	Partition	Best-fit model
CytB	1st + 2nd nucleotide positions	GTR+F+I
	3rd nucleotide position	GTR+F+I
ND1	1st nucleotide position	K2P+FQ+G4
	2nd nucleotide position	HKY+F+I
	3rd nucleotide position	HKY+F

In addition, a number of published sequences from the GenBank database were used for comparison, including sequences of the European *E. serotinus* bearing alien mtDNA from *E. nilssonii* (see Artyushin *et al.*, 2009). Their accession numbers are listed below.

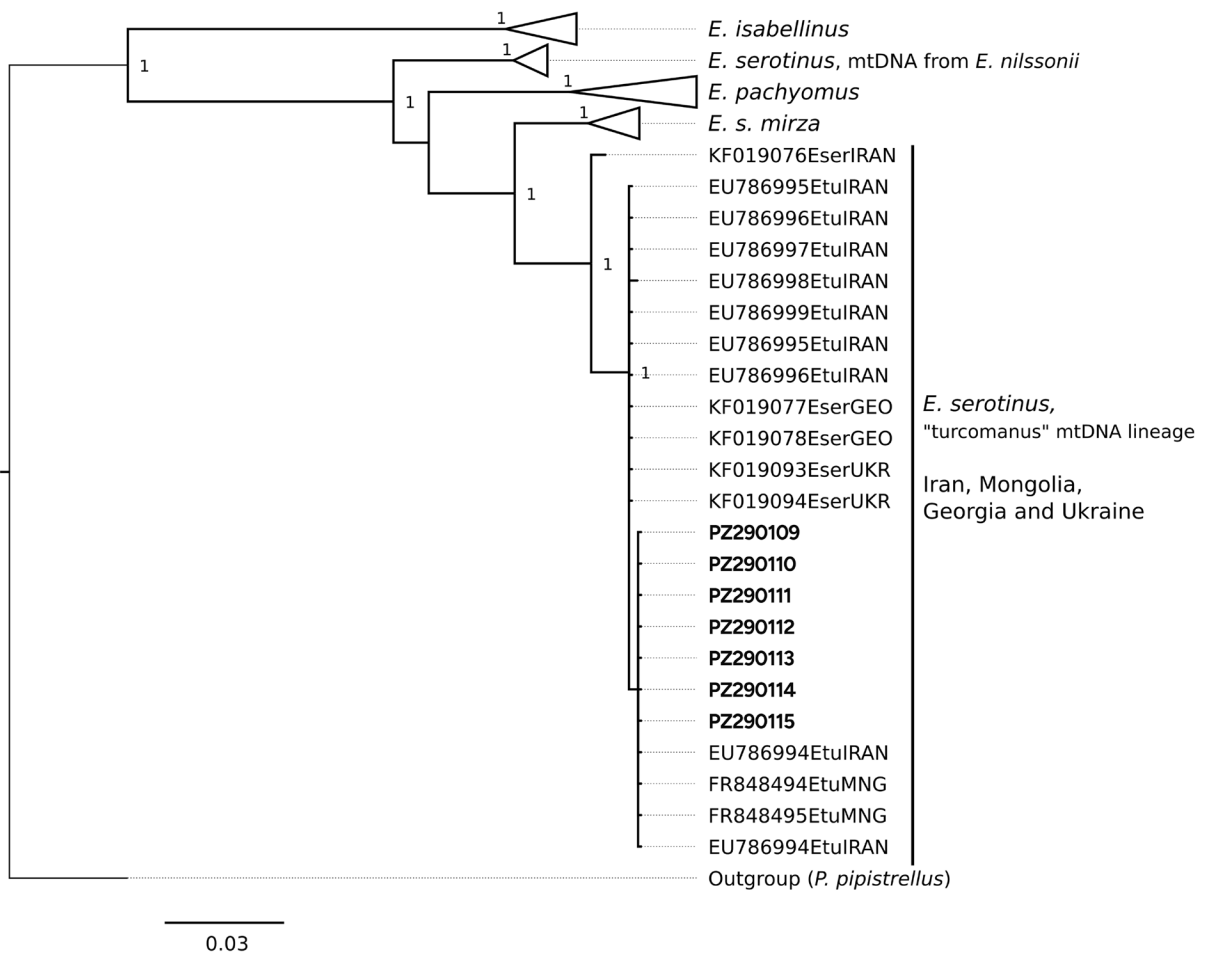


Fig. 2. Phylogenetic relationships between large Eurasian *Eptesicus* species and position of the Mongolian specimens based on sequences (665 bp) of the mitochondrial ND1 gene, according to Bayesian analysis. Numbers at nodes denote posterior clade probabilities, only values above 80% are shown. Specimens in bold were genotyped in this study.

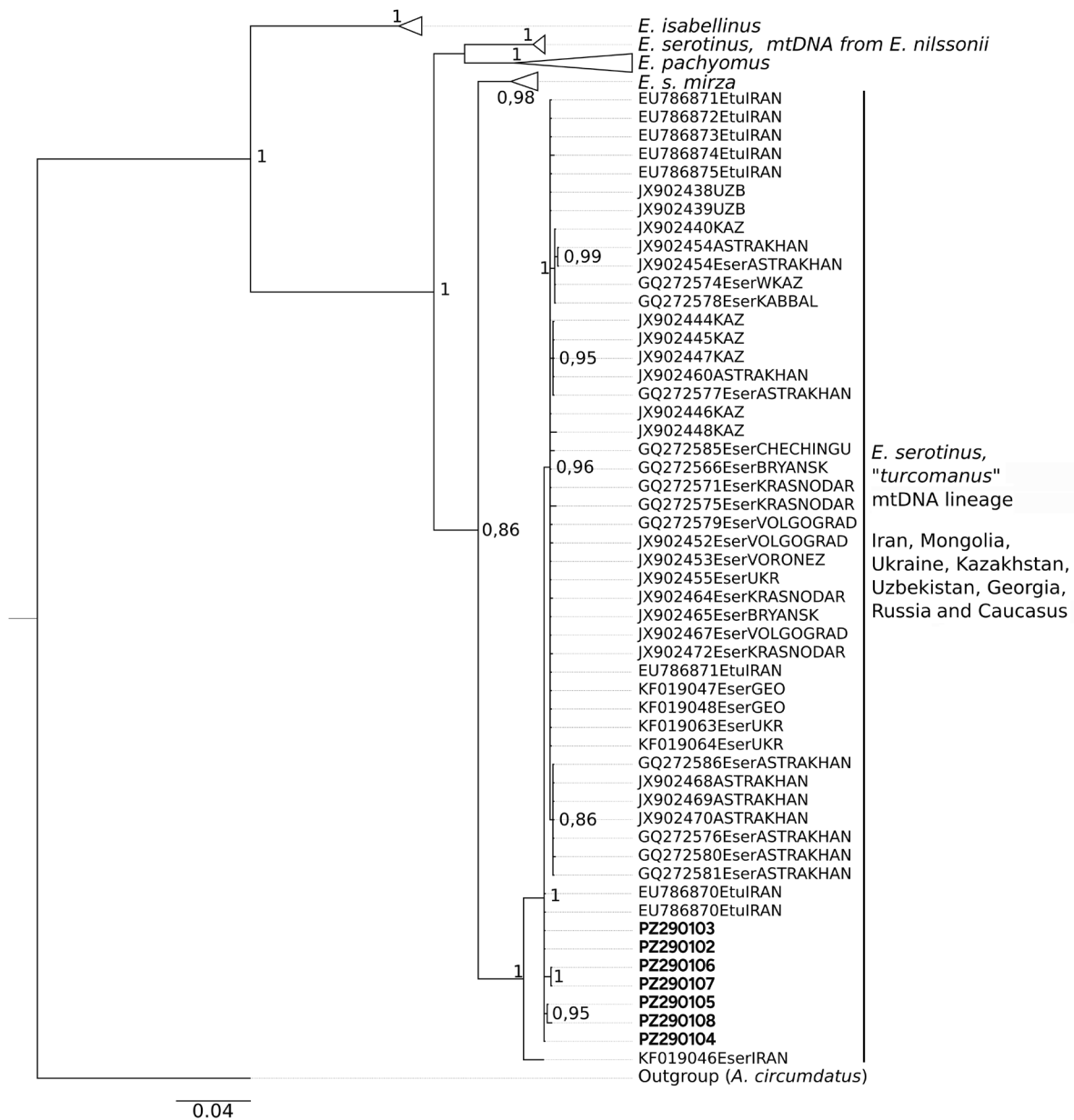


Fig. 3. Phylogenetic relationships between large Eurasian *Eptesicus* species and position of the Mongolian specimens based on sequences (1140 bp) of the mitochondrial CytB gene, according to Bayesian analysis. Numbers at nodes denote posterior clade probabilities, only values above 80% are shown. Specimens in bold were genotyped in this study.

Cytochrome B: GQ272566, GQ272585, GQ272586, GQ272571, GQ272574–GQ272581, GQ272587 (Artyushin *et al.*, 2009); JX902438–JX902440, JX902444–JX902448, JX902454, JX902460, JX902468–JX902470, JX902452–JX902459, JX902464–JX902467, JX902472 (Artyushin *et al.*, 2012a); AF376837 (Ruedi, Mayer, 2001); MF187881–MF187955 (Troupin *et al.*, 2017); MG570068; OP157123, (Yi *et al.*, 2024); DQ120832–DQ120839 (Ibáñez *et al.*, 2006); EU786824–EU786838, EU786841–EU786863, EU786870–EU786875, KF019046–KF019050, KF019063, KF019064 (Juste *et al.*, 2013);

KF218369–KF218374 (Çoraman *et al.*, 2013); ON369433 (Zhang *et al.*, 2018); ON310508 (Tiunov *et al.*, 2023).

ND1: ON310507 (Tiunov *et al.*, 2023); EU786948–EU786962, EU786965–EU786987, EU786994–EU786999, KF019076–KF019080, KF019093, KF019094 (Juste *et al.*, 2013); AF401471, AF401472 (Mayer & von Helversen, 2001); AY033950 (Ruedi & Mayer, 2001); DQ120803, DQ120804 (Ibáñez *et al.*, 2006); DQ915023, DQ915024 (Mayer *et al.*, 2007); KF218437–KF218441 (Çoraman *et al.*, 2013).

Results and discussion

Sequences for all seven specimens, both for ND1 and CytB genes (available at NCBI, accession numbers PZ290102-PZ290115) were obtained and then compared with the previously published ones. In total the final alignment for ND1 included 73 unique sequences and for CytB — 191.

Using Bayesian methods, we obtained the phylogenetic trees for both of the considered loci (Figs 2 and 3). The overall grouping of the sequences from the previously published material showed no significant divergence, compared to the results of the previous studies that used them. In both trees the most basal positions (excluding the outgroups) was taken by the *E. isabellinus* clade. The positions of sequences assigned to *E. serotinus* or *E. pachyomus* were somewhat different between ND1 and CytB trees. The sequences of *E. serotinus* specimens, having introgressed mtDNA from *Eptesicus nilssonii* (Artyushin *et al.*, 2009, 2012b) took basal positions in relation to other *E. serotinus* (representing *E. s. mirza*, and *E. s. turcomanus* mitochondrial lineages) and *E. pachyomus*, which is concordant with the previously published results. All other sequences in the analyses were allocated to the clades of *E. serotinus* which we may tentatively call *E. s. mirza* and *E. s. turcomanus* lineages. Our specimens belong to the latter clade, grouping tightly together. Thus, our data support the attribution of the Mongolian specimens to the *E. serotinus* s. str. lineage and not to the *E. pachyomus* lineage.

Serotines are currently known from seven localities in Mongolia (Fig. 1; Table 1). These locations are situated in southern part of the country, in the Omnogovi aimag (Province). All the Mongolian records were made in or near the Gobi Desert, which has arid climate and barren landscape, however, the capture localities were situated within oases or in their close vicinities. Our samples were collected at sites situated between the previously known *E. serotinus* capture sites, enriching our knowledge of the distribution range of the large serotines in Mongolia. Phenotypically, the studied Mongolian specimens resemble *E. serotinus* individuals from arid places of Lower Volga or Kazakhstan. All sequences of the Mongolian specimens, both our and published previously, grouped together and were placed within the *E. s. turcomanus* genetic lineage. Generally, the Mongolian population of *E. serotinus* is relatively homogenous genetically, at least when using the analyzed mitochondrial markers. This can also apply to the whole lineage, as the haplotypes from the western part of its range (for example, from Astrakhan, Bryansk and Voronezh, taken from Artyushin *et al.*, (2012b) and probably representing genuine *E. serotinus* mtDNA (see Artyushin *et al.*, 2018)) are mixed up with the Asian ones, thus implying low phylogeographic structure within this taxon.

Old records of the large *Eptesicus* from Central Asia were affiliated by Bobrinskoj (1929) to *E. serotinus turcomanus*; the latter author also supposed that the

names *turcomanus* and *pallens* (*pallidus* in Bobrinskoj, an error) could be synonyms. Allen (1938) considered *E. s. pallens* distinct from *E. s. turcomanus* and allocated all the aforementioned Central Asian records to the former name. Apparently, this is what gave rise to the idea of the inclusion of the south of Mongolia in the range of *E. serotinus pallens* (and later — *E. pachyomus pallens*). Later it has received support from the publication of Juste *et al.* (2013), which included the distribution map published with *E. p. pallens* type locality erroneously depicted on the very north of Gansu (or even in Xinjiang), close to the Mongolian state border. However, the original terra typica was published as “Cheng Yuan Hsien, 70 mi W of Ching Yang Fu” by Miller (1911). It is currently interpreted as Qingyang, Gansu (Orrell, 2026). This site is situated at about 670 km south from the Mongolian state border (Fig. 1).

However, although there are just about 250 km between “*pallens*” type territory and the location of the specimen from Shaanxi (Daguping, Foping County), which was sequenced as “*E. p. pallens*” by Juste *et al.* (2013), these two points are situated in quite different natural conditions. The latter specimen was captured on the southern slope of the Qinling Mts., covered with a montane forest. This area represents a transitional zone between the Central Asian temperate climate and the humid subtropical climate (Zhao *et al.*, 2020). On the other hand, vicinities of Qingyang, including “*pallens*” type locality, are situated north from the Qinling Mts. and represented by the Loess Plateau, with significantly drier (semi humid) and colder climatic conditions (Wang *et al.*, 2006; Kapp *et al.*, 2015). This climate shift casts doubt on whether the serotines of these two areas belong to the same taxon. Given the general range of conditions, in which both species of the large Eurasian *Eptesicus* can thrive, this cannot be ruled out. However, it is also possible that the name *pallens* is actually a junior synonym of *E. serotinus*, not of *E. pachyomus*. Only a study of specimens (including the molecular genetic approach) from the type area can definitively clarify these issues.

Thus, we can conclude that the attribution of the Mongolian specimens of the large *Eptesicus* to *E. pachyomus* by Batsaikhan *et al.* (2022) was based on an erroneous interpretation of the distribution range extent of this species, and actually only *E. serotinus* occurs in Mongolia. The range of *E. serotinus* in Central Asia is most probably located in more northern areas with arid or semiarid climate and does not enter the mountainous regions of central China. Conversely, the northern limit of the range of *E. pachyomus* does not extend northwards into arid regions and likely does not approach the territory of Mongolia.

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