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ORIGINAL PAPER

Phylogeography, morphometry and the species distribution modelling in *Myotis longicaudatus* (Chiroptera, Vespertilionidae) in the Eastern Palaearctic

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Abstract

The long-tailed myotis, *Myotis longicaudatus*, is considered one of the rarest bat species in the northeastern Palaearctic. Originally considered a subspecies of *M. frater*, was elevated to species level in 2015 based on molecular differentiation. Currently, three subspecies are recognized based on morphometric data. This study aimed to identify the geographic patterns of the population genetic structure and morphological variability of *Myotis longicaudatus* throughout its range, and also to find out whether they are related to environmental parameters. The species distribution modelling based on the subsets of twenty environmental variables for two mainland subspecies of *M. longicaudatus* predicted that *M. l. eniseensis* is distributed westward from the Greater Khingan Mountains, and *M. l. longicaudatus* eastward. Except for Transbaikalia, capture sites were predominantly located in two land cover classes: deciduous broad-leaved and needle-leaved forests. Population genetic analyses based on *cyt b* sequences identified a split into the Eastern (corresponded to the morphological subspecies *M. l. longicaudatus* and *M. l. kaguyae*) and the Western (corresponded to the morphological subspecies *M. l. eniseensis*) haplogroups. The *p*-distance between the two main haplogroups was 0.92% and between the mainland and island samples of the Eastern haplogroup 0.47%. Two haplotypes of the Western haplogroup were most widely distributed in Siberia, the E8 haplotype was distributed in Western and Central Siberia, and the E4 haplotype in Eastern Siberia (Baikal Region and Transbaikalia). We recorded *M. longicaudatus* in Transbaikalia for the first time. Morphometric analyses showed the greatest differences between eastern (*M. l. longicaudatus* and *M. l. kaguyae*) and western (*M. l. eniseensis*) *M. longicaudatus*. The specimens from Transbaikalia were similar to eastern *M. longicaudatus* in morphometric parameters. Molecular and morphometric data converge and do not contradict the presence of three subspecies, but overall variability within the species being quite low.

Keywords Long-tailed myotis · Phylogeography · Haplogroup · Genetic diversity · Species' range · Morphometry

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Introduction

The long-tailed myotis, *Myotis longicaudatus* Ognev 1927, had been originally described from the Russian Far East as a distinct species (Ognev 1927, 1928), but later was considered a subspecies of *M. frater* G.M. Allen, 1923 based on the similarity of published measurements (Ellerman and Morrison-Scott 1951). For decades, *M. frater* was thought to have wide but disjunct range covering Central Asia (Tajikistan and Uzbekistan), Siberia, the Far East, Japan, Southeast China, and Taiwan (Koopman 1994). Correspondingly, four subspecies were thought to inhabit each of major parts of the range: *M. f. bucharensis* Kuzyakin, 1950, *M. f. longicaudatus* Ognev 1927, *M. f. kaguyae* Imaizumi 1956, and *M. f. frater* s. str., respectively (ibid.). Later the subspecies *M. f. bucharensis* was raised to full species *M. bucharensis* based on morphometric analysis (Tsytsulina and Strelkov 2001), which was then confirmed by genetic data (Kazakov et al. 2020). At the same time, Siberian populations were described as an additional subspecies, *M. f. eniseensis* (Tsytsulina and Strelkov 2001). More recently, molecular analysis showed that boreal-temperate and tropical (Taiwan) taxa of *M. frater* s. l. are different species and the oldest available name for the boreal-temperate taxon is *M. longicaudatus* Ognev 1927 (Ruedi et al. 2015). This study also identified a new species *M. soror* from Taiwan also closely related to *M. frater*. Distinctiveness of *M. frater* and *M. longicaudatus* was then confirmed by morphometric data (Kazakov et al. 2020). Finally, a new part of the range, probably inhabited by a new undescribed taxon from the *M. frater* species complex, was revealed in the northern India (Chakravarty et al. 2020).

Frater-like *Myotis* were thought to belong to the "*daubentonii*" species group ("clade III") based primarily on mtDNA data and one nuclear marker Rag2 (Ruedi et al. 2013; Kazakov et al. 2020). However, nuclear DNA data (Morales et al. 2019) do not support this view, though position of the frater-like *Myotis* in the latter work is highly questionable. Nonetheless, taking the present controversy into account, here we avoid using the term "species group" and prefer the rank-free informal term "species complex".

M. longicaudatus, particularly within its mainland range, remains one of the least studied bat species in the Palaearctic, with limited information on its genetic variability and intraspecific structure. *COX1*-barcoding of mainland specimens (formerly "*M. frater*") revealed two distinct clades corresponding to the morphological subspecies *M. l. longicaudatus* and *M. l. eniseensis*. However, this study relied on a small sample size and did not include data from insular populations (Kruskop et al. 2012). It is believed that the *M. longicaudatus*' range consists of several separate clusters, the longest gaps between which are located in the Eastern Sayan Mountains and Transbaikalia (Tsytsulina and Strelkov 2001; Kruskop 2012).

At present, the phylogeography of just few widespread bat species has been studied in the Palaearctic. In most cases, these studies covered only the Western Palaearctic. For example, studies of the phylogeography of *Plecotus macrobullaris* and *P. austriacus* based on complete mitochondrial genomes and the mitochondrial *cyt b* gene, respectively, showed the divergence into two main lineages for each of the species (Razgour et al. 2013; Alberdi et al. 2015). Much less research is devoted to the phylogeography of bats in the Eastern Palaearctic, due to the large area of the region, the inaccessibility of many areas, the cold climate, and the lower diversity of bats. However, a number of bat species are distributed only in the northeastern Palaearctic, highlighting the relevance of research in this region. Several studies of the intraspecific variability of *M. davidii* Peters, 1869 (including those referring to it as "*M. aurascens*") have also demonstrated the presence of two main clades distributed to the west and to the east of the Tien Shan Mountains, respectively (Kruskop et al. 2012; Çoraman et al. 2020). *M. davidii* is one of the few studied bat species distributed both in the Western and Eastern Palaearctic. In addition, Park et al. (2019) showed quite high genetic diversity of *M. ikonnikovi* populations in Korea comparable to that of *M. myotis*, *M. lucifugus*, and *M. septentrionalis*.

While *M. longicaudatus* has quite large range, until recently it was thought to be a rare species and its genetic diversity and phylogeography were almost unstudied. The only data on this subject were published by us in the context of the taxonomic study of *M. bucharensis* (Kazakov et al. 2020). The purpose of the present study is to fulfill this gap in knowledge and identify the geographical patterns of the population genetic structure and morphological variability of *M. longicaudatus* throughout its range, as well as to try to model the species distribution.

Materials and Methods

Bat Sampling

Bats were caught in June at summer roost, in July at foraging sites, in April and August at swarming sites (at the cave entrances) using mist nets (7.0 m × 2.5 m, 9.0 m × 2.5 m, 16 mm; *Ecotone*, Poland) in 1999, 2000, 2003, 2014 and from 2018 to 2022. Original photographs of some captured specimens are shown in Fig. 1. The sampling sites are

Fig. 1 *M. longicaudatus* from Altai Krai, Logovo gieny Cave, 23 ▶ June 2020 (a), and Transbaikal (Zabaikalsky) Krai, Lurgikanskaya Cave, 21 August 2021 (b). Photo by Denis V. Kazakov


a
b

located in different regions of Russia and Japan (Fig. 3a, Supplementary Information: Table S1). Bat wing membrane biopsies were sampled using a 3 mm skin biopsy punch and preserved in 96% ethyl alcohol at + 4 °C until DNA extraction. Afterwards, the bats were ringed with aluminum rings (measuring 2.9 mm) and released at their capture site the following evening. Tissue samples (muscle) from bat vouchers (carcasses fixed in ethanol) deposited at Zoological Museum of Lomonosov Moscow State University (*ZMMU*, Moscow), and «Siberian Zoological Museum, Novosibirsk» of Institute of Systematics and Ecology of Animals (Siberian Branch of the Russian Academy of Sciences; *SZMN ISEA*) were also used. A total of 36 field-collected samples and 15 samples from repositories (13 samples from *ZMMU* and 2 samples from *SZMN ISEA*) were analyzed. All applicable international, national and institutional ethics statements for using animals in research have been followed.

Species distribution modelling

We used the Maxent 3.4.4 (Phillips et al. 2006) algorithm and 19 environmental variables from WorldClim 2.1 database (https://worldclim.org/data/worldclim21.html) with 2.5 arcmin resolution to generate environment suitability maps for the Eastern Palaearctic. The SDM-modelling was based on 87 presence location records of *M. longicaudatus* from across the species' range: 36 for *M. l. eniseensis*, 22 for *M. l. longicaudatus* and 29 for *M. l. kaguyae* (Supplementary Information: Table S2) obtained from valid publications and repositories (ZMMU, ZIN RAS, SZMN ISEA; explanation of acronyms provided earlier). The same data were used to assess the calibrating range for all models, which ended up being limited to known range of the species. The models were generated separately for each subspecies, as the combined model had a lower predictive ability (AUC = 0.89, SD = 0.025). Stability of the models was assessed by conducing 20 replications by subsampling. To evaluate the model, we used random 20% of capture sites as a test sample across the selected training area. For all models we used default settings with the edition of "random seed" turned on. We iteratively excluded variables, with the least contribution according to jackknife test, unless total test-sample AUC started to drop by more than one SD of AUC between replications. The following environmental variables were included in the final models: for *M. l. eniseensis*—annual mean temperature (BIO1), isothermality (BIO3), temperature seasonality (BIO4), maximum temperature of warmest month (BIO5), mean temperature of wettest quarter (BIO8), mean temperature of warmest quarter (BIO10), Mean Temperature of Coldest Quarter (BIO11), Annual Precipitation (BIO12), precipitation of wettest month (BIO13), precipitation of driest quarter (BIO17) and precipitation of warmest quarter (BIO18); for *M. l. longicaudatus* – BIO1, mean diurnal range (mean of monthly (max temp—min temp)) (BIO2), BIO3, BIO4, BIO8, BIO10, BIO12, BIO13, precipitation of driest month (BIO14), precipitation seasonality (BIO15), precipitation of wettest quarter (BIO16) and BIO18; for *M. l. kaguyae* – BIO1, BIO2, BIO4, BIO8, mean temperature of driest quarter (BIO9), BIO11, BIO14, precipitation seasonality (coefficient of variation) (BIO15), BIO16, BIO17 and precipitation of coldest quarter (BIO19). We also used Copernicus Land Cover data (Buchhorn et al. 2019) to assess biome preferences of subspecies separately from subspecies distribution modelling.

DNA extraction, amplification and sequencing

Genomic and mitochondrial DNA were isolated from wing membrane biopsy samples and muscle using the *Diatom DNA Prep 200 Kit* (Isogene Lab., Moscow, Russia), according to the manufacturer's protocol with modifications as described in Kazakov et al. (2020). The complete mitochondrial cytochrome b gene (*cyt b*) (1140 bp) was amplified using the primer pair Molcit-F 5'-AATGACATGAAA AATCACCGTTGT-3' (Ibañez et al. 2006) and BSves268H 5'-ATTTCTGGYTTACAAKACCRGTGTAA-3' (Stadelmann et al. 2004). For the PCR reaction, the 20 µl PCR mix contained 4.0 µl of 5 × PCR buffer (1.0 × : 3.5 mM $MgSO_4$), 0.4 µl of dNTPs (10 mM each; 0.2 mM), 0.1 µl of each 100 µM forward and reverse primers, 0.3 µl of 50 × Encyclo polymerase Mix (0.75 ×), and 1.0 µl of DNA template per sample. Milli-Q water was used to make up the remaining volume. The following thermal profile was used: initial denaturation of 4 min at 94 °C, followed by 35 cycles of 30 s at 94 °C, 30 s at 53 °C, 90 s at 72 °C, with a final extension of 10 min at 72 °C (Stadelmann et al. 2007). All final PCR products were visualized on 1.0% agarose gels, purified using the *Cleanup S-Cap Kit* (Evrogen JSC, Russia), and sequenced in both directions using the ABI BigDye Terminator v 3.1 Cycle Sequencing Kit with the same primers and run on the ABI 3500 Genetic Analyzer.

Phylogenetic and Population genetic analyses

The original sequences are deposited in the GenBank under accession no. MT547884–MT547901, ON456086-ON456115, and OQ785258-OQ785259. The sequences were aligned with published *M. longicaudatus* sequences from the GenBank (KX467612, FJ215682, AB106593, NC_041638) using the CLUSTAL algorithm (Sievers et al. 2011). Maximum likelihood reconstruction was conducted in the IQTREE v. 1.6.12 software (Nguyen et al. 2015) with 1000 bootstrap replicates to test topology stability. The ModelFinder (Kalyaanamoorthy et al. 2017) was used to select the optimum partitioning scheme and the best-fit substitution model under BIC criterion. The *M. bucharensis* and *M. frater* sequences (MT547883, KP187872)

from the GenBank were used as outgroups. Median-joining haplotype network were constructed using the NETWORK v. 10.2 (https://www.fluxus-engineering.com/). We performed an analysis of molecular variance (AMOVA) and computed pairwise F_{ST} in ARLEQUIN v. 3.5 (Excoffier and Lischer 2010). Metrics of genetic diversity (haplotype diversity, nucleotide diversity, theta-W per sequence and average number of nucleotide differences) were computed using DnaSP 6.12 (Rozas et al. 2017). Genetic distances were estimated using MEGA v. 11 (Tamura et al. 2021).

Morphometric analyses

Although a preliminary morphometric analysis of *frater*-like *Myotis* was performed by us earlier (Kazakov et al. 2020), here we focused especially on *M. longicaudatus*, expanding the previous sample of this species and excluding other related forms. Measurements were taken with digital calipers S_Cal PRO under binocular microscope to the nearest 0.01 mm. A total of 92 M. *longicaudatus* specimens (skulls, extracted from dry or alcohol preserved skins) were measured; this set was later reduced to 85 specimens (including holotypes of all three accepted subspecies) due to missing data (damages in measured parts of some skulls), and further analyzed. The full list of these specimens is provided in the Supplementary Information (Table S3). Acronyms of repositories of the processed collections are as follow: AOPM – Aomori Prefectural Museum (Aomori, Japan); NMSN – National Museum of Science and Nature (Tokyo/Tsukuba, Japan); DK – D. Kazakov work collection, University of Tyumen (Tyumen, Russia); KK – K. Kawai work collection, Tokai University (Sapporo, Japan); ZMMU – Zoological Museum of Moscow State University (Moscow, Russia); ZIN RAS – Zoological Institute, Russian Academy of Sciences (St. Petersburg, Russia).

The following cranial measurements (abbreviations given in parentheses) were taken: condylobasal length (CBL), condylocanine length (CCL), occiput height from the lower margin of condyles to the occiput-parietal suture (OH), mastoid width of skull at the level of the auditory bullae (MW), width of braincase (BCW), least width of the postorbital constriction (POW), rostral width at the level of the infraorbital foramina (RW), rostral length from anteorbital foramen to the alveolus of the inner incisor (RL), C–M3 length (CM3), maxillary molariform row length (P4M3), length of the upper canine cingulum base (C), length of interval between cingula of upper canine and large premolar ("pseudodiastem", Pseud), crown-measured width between the outer margins of upper canines (CC), crown-measured width between outer margins of M3 (M3M3), crown width of M3 (wM3), crown length of M3 (lM3), crown width of M2 (M2), lower jaw length from alveolus of i1 to the posterior extremity of glenoid process (MdLg), lower jaw length from alveolus of i1 to the posterior extremity of angular process (MdLa), crown length of mandibular tooth row (cm3), crown length of mandibular molariform row (p4m3), lower jaw height to the tip of coronoid process (MdH). This set of measurements was adopted by us from earlier taxonomic studies (e. g. Yoshiyuki 1971; Benda and Horáček 1995; Topál 1997), with additions, and then used in multiple studies on taxonomy of another *Myotis* species (Matveev et al. 2005; Kruskop 2013; Kruskop et al. 2018; Kruskop and Solovyeva 2021).

To assess the pattern of variation of quantitative characters, Principal Component (PC) and Discriminant Function (DF) analyses were performed for the 22 craniodental measurements, using the appropriate modules of STATISTICA for Windows version 7.0 (StatSoft, Inc., 2004). DF analysis was used to calculate the squared Mahalanobis distances between groups and the significance of inter-group difference. The training set for calculating Squared Mahalanobis distances and Posterior probabilities within the DF analysis included five geographical samples, namely "northern Honshu" (= Tohoku Region), "central and western Honshu", "Hokkaido", "Primorye", and "central-southern Siberia". Specimens from Transbaikalia, the Tunkinskie goltsy Range, Sakhalin and Kunashir (Kunashiri), as well as few specimens with unknown localities within Honshu, were included into analysis as undetermined. The division of the specimens from Honshu into two samples was dictated, on the one hand, by the relatively large volume of material from this region (39 specimens in the analysis, more than in any other geographical sample). On the other hand, using such sample size, we wanted to test if animals living in northern and southern Honshu, with reliably different climate, would differ from each other. Since the animals from different geographical samples are similar in size (none of them are significantly larger or smaller), analyzes were performed with raw untransformed data. Both male and females were present in the whole measured set, but with high disproportion between different geographic samples (e. g. no females were in the sample from central and western Honshu, only one male was present in each of Hokkaido and Primorye samples). Preliminary analysis of the whole set did not show sexual dimorphism within the species ($p > 0.3$), so division by sexes was excluded from the final analyzes.

Results

Species distribution modelling

For *M. l. kaguyae*, our model had high AUC of 0.99 (SD = 0.004), however the test omission rate had large standard deviation, and according to the jackknife test, the most impactful was the Mean Temperature of Coldest Quarter

(BIO11) parameter, which could mean a bias towards it, given the small number of animal records available. Even after the significant reduction of analysed area (together with training area) the same picture remained, except the test omission rate was close to the predicted omission rate this time and AUC had lower values (AUC = 0.93, SD = 0.017). With that in mind, the predicted distribution of the subspecies was limited to Japan, Sakhalin and Kunashir Islands in both models, which resembles its known distribution with no additional significant information added. Therefore, we focused on the models for the mainland subspecies. Separated models for the two mainland subspecies (Fig. 2) had higher predictive ability, AUC = 0.96 (SD = 0.018) and AUC = 0.92 (SD = 0.03) for *M. l. longicaudatus* and *M. l. eniseensis*, respectively, compared with the combined model (AUC = 0.89, SD = 0.025). Capture sites for both subspecies were located predominantly within the land cover class DBF (deciduous broad leaf forest, class 114 in Buchhorn et al. 2020a, b). We observed a separation of the two subspecies ranges with a border roughly coinciding with an edge of the DBF range gap in Transbaikalia. According to the models, *M. l. longicaudatus* is distributed to the east of the Greater Khingan Mountains and *M. l. eniseensis*, to the west. All capture sites were within the suitable area.

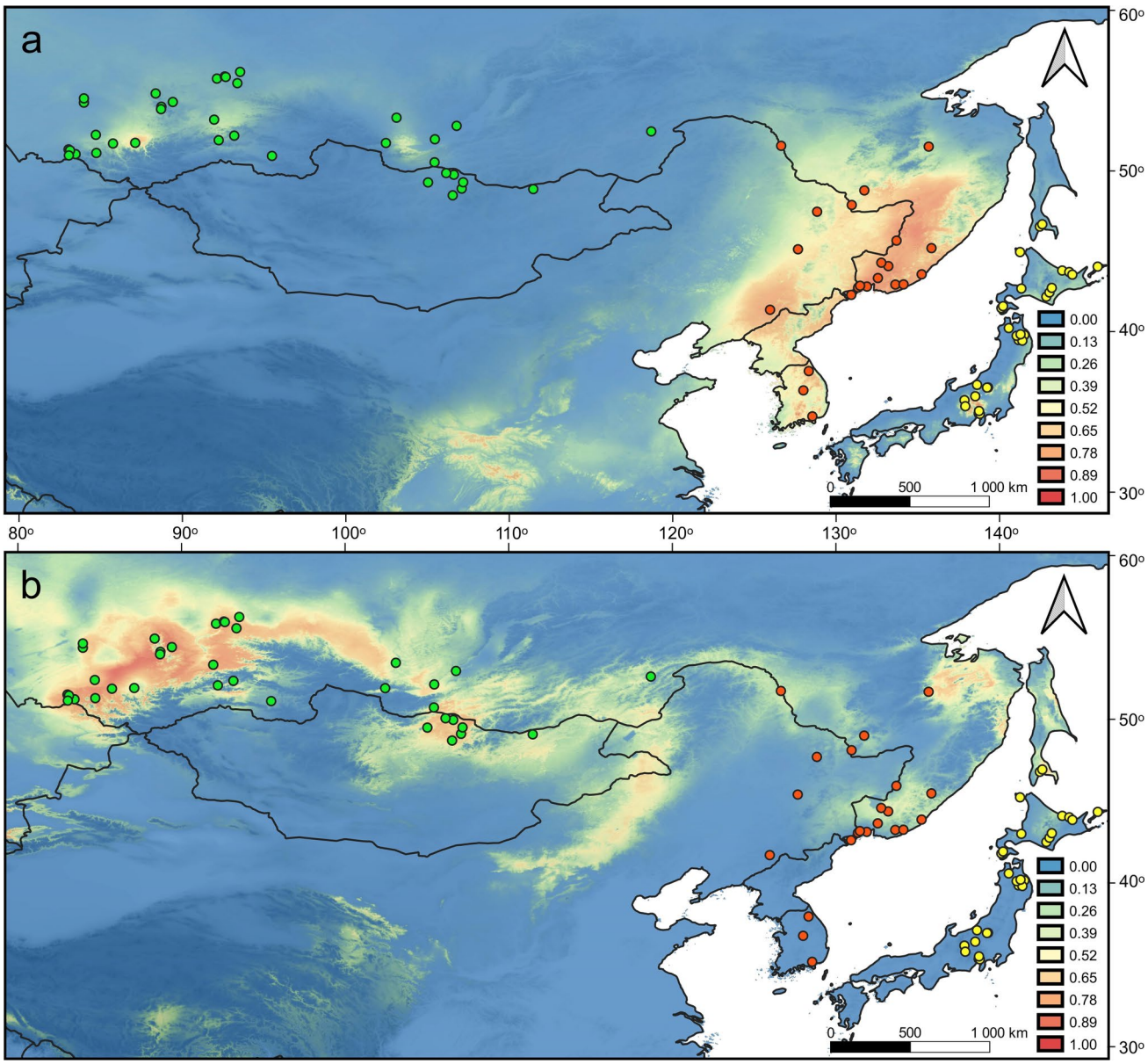

Fig. 2 The SDMs showing the predicted current distribution of suitable climatic conditions for *M. l. longicaudatus* (a, red sites) and *M. l. eniseensis* (b, green sites) in the Eastern Palaearctic. Yellow sites – *M. l. kaguyae*

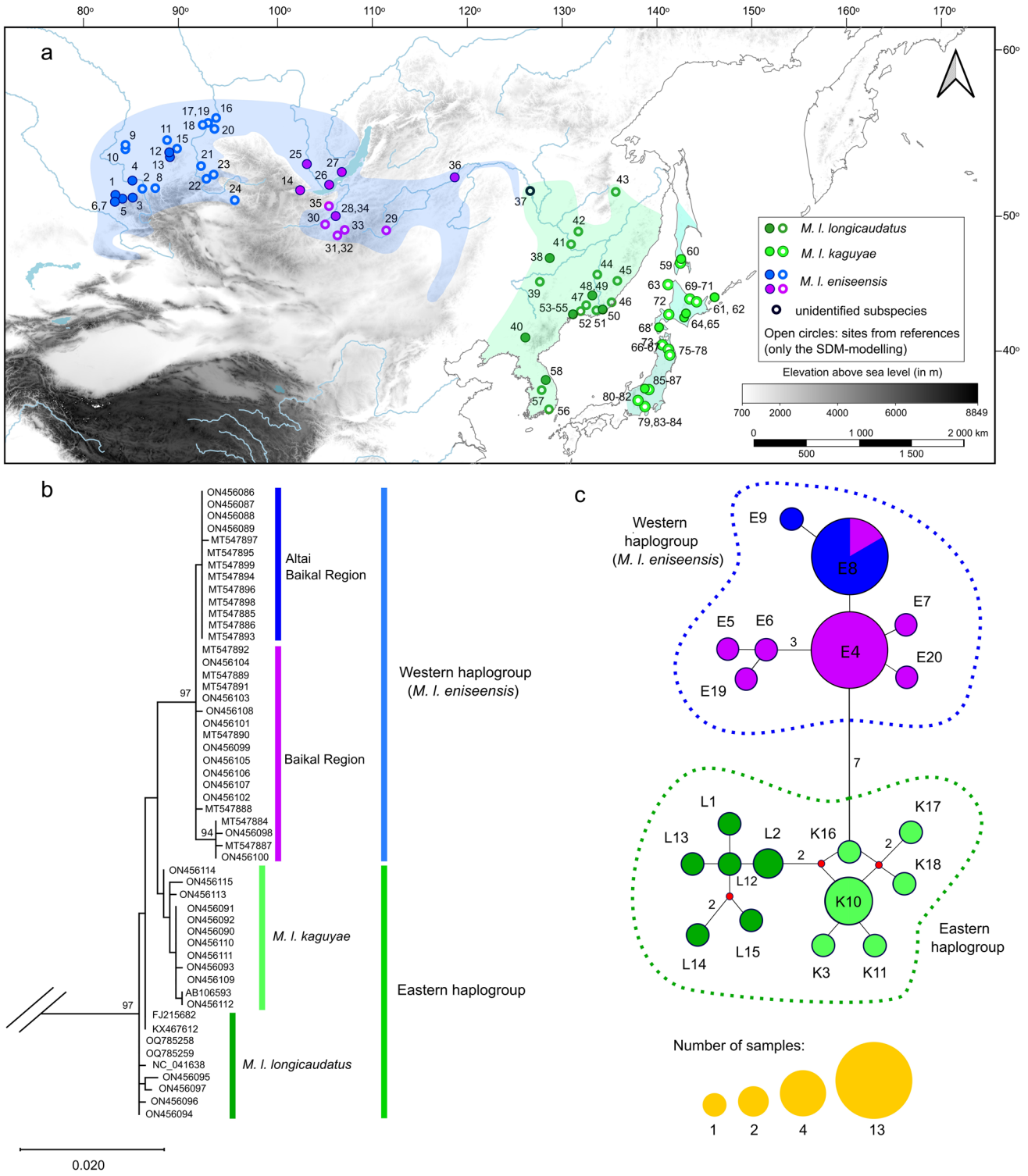

Fig. 3 Map showing the approximate ranges of *M. longicaudatus* subspecies (blue and green shaded areas) from the SDM-modelling, sampling sites and sites of records from references. The explanation of site numbers is given in the Supplementary Information, Table S1 and S2 (a); hydrography and terrain data source: ESRI, Open Street Maps (Adjusted); Projection: WGS 84. Maximum likelihood (ML) tree based on 55 *cyt b* sequences (1140 bp) of *M. longicaudatus* and outgroups (b), and Median-joining network of *cyt b* haplotypes in *M. longicaudatus* (c); colour-coded based on their geographical areas; circle size corresponds to number of samples, and numbers represent connections separated by more than one mutation

The most prominent clusters of suitable conditions outside of the previously known ranges of the subspecies were predicted in Sakhalin Island, Primorsky Krai and Low Amur for *M. l. eniseensis*, and in Honshu, Kyushu, CE China and Upper Ob River (Russia) for *M. l. longicaudatus*. The cluster in Primorsky Krai for *M. l. eniseensis* had low suitability values, and the cluster in the Low Amur did not overlap with the SDM for *M. l. longicaudatus* in this region. The model for *M. l. eniseensis* using data for 1960–1990 from WorldClim 1.4 showed the cluster in the Lower Amur with smaller area and lower suitability values. The cluster in CE China (Hubei, Shaanxi, Henan Provinces and Chongqing) for *M. l. longicaudatus* was 1500 km away from the known capture sites of the subspecies.

The SDM for *M. l. eniseensis* was heterogeneous, so the proportion (= area) of suitability values of 0.65–1.00 was higher in Western and Central Siberia (to the Yenisei River valley) compared to Baikal Region and Transbaikalia, where suitability values less than 0.65 prevailed.

Phylogenetic and Population genetic analyses

The phylogenetic analysis of the mitochondrial *cyt b* gene revealed the basal position of *M. l. longicaudatus* within the species with a high bootstrap support (97%). Mostly the nodes on the ML tree had low bootstrap supports, the only clade with a high bootstrap support (97%) was *M. l. eniseensis*. Within the clade *M. l. eniseensis* is a subclade with a high bootstrap support (94%), including samples from Baikal Region and Transbaikalia (Argaley-3, Okhotnichya, Mechta and Lurgikanskaya Caves). Median-joining network showed the split into two main haplogroups, Eastern and Western, included 20 haplotypes across the species' range (Fig. 3). The majority of haplotypes were separated by only one mutational step. The AMOVA analysis (by pairwise differences) showed that 69.67% of the genetic variation were caused by differences between the two main haplogroups, while inter- and intra-population variation explained 18.30% and 12.03% of the genetic variation, respectively. Genetic differentiation between the two main haplogroups was 0.918% (0.927% K2P), between mainland and island samples of the Eastern haplogroup was 0.465%, and among populations was high ($F_{ST} = 0.879$) and significant ($p = 0.000$). The pairwise F_{ST} values were 0.664–0.714 ($0.000 \leq p \leq 0.006$) between mainland and different island populations of the Eastern haplogroup, and 0.439 ($p = 0.000$) among populations of the Western haplogroup. Diversity indices (Table 1) indicated a higher genetic diversity in the Eastern haplogroup compared to the Western haplogroup. The results of neutrality (Tajima's D and Fs) tests for each haplogroups were not significant.

Eastern haplogroup

The approximate range according to the SDM-model on the mainland includes the Korean Peninsula, the Songliao Plain (Liaoning, Jilin and Heilongjiang Provinces of China), the Sikhote-Alin Mountains (Primorsky Krai of Russia) and the basin of the middle and low reaches of Amur River. Insular populations are distributed in Honshu, Hokkaido, Sakhalin, Kunashir (Kuril Islands) and Rishiri Islands. The individuals caught in the northern and southern parts of the Songliao Plain at a distance of 700 km from each other belonged to the same haplotype. At the same time, four unique haplotypes were found in southern Primorye within a radius of 150 km. We identified three unique haplotypes in Honshu, two haplotypes in Hokkaido, one of them was also recorded in Kunashir.

Western haplogroup

The haplogroup range stretches from the Northwestern Altai Mountains and the upper reaches of Ob River to the east to the Greater Khingan Mountains, to the south including the taiga zone and the adjacent forest-steppe areas in Mongolia.

Table 1 Genetic diversity of *M. longicaudatus* haplogroups and the results of the neutrality tests based on the *cyt b* mtDNA gene

№	Indices and neutrality tests	*Eastern haplogroup*	*Western haplogroup*	Total
1	Number of sequences	21	31	52
2	Number of polymorphic sites, S	16	9	31
3	Number of haplotypes, h	12	8	20
4	Haplotype (gene) diversity, Hd ± SD	0.905 ± 0.05	0.714 ± 0.05	0.885 ± 0.03
5	Nucleotide diversity, Pi ± SD	3.12 ± 0.38 $\times 10^{-3}$	1.36 ± 0.29 $\times 10^{-3}$	5.48 ± 0.39 $\times 10^{-3}$
6	Average number of nucleotide differences, k	3.495	1.523	6.145
7	Theta (per sequence) from S, Theta-W	4.447	2.253	6.860
8	Tajima's D test	−0.786 $p > 0.1$	−0.999 $p > 0.1$	−0.346 $p > 0.1$
9	Fu's test, F_s	−4.088 $p = 0.012$	−2.197 $p = 0.062$	−3.242 $p = 0,020$

Table 2 Selected cranial and dental measurements (min–max, mean ± standard deviation) of *Myotis longicaudatus* samples. See measurement abbreviations in the text

	M. l. longicaudatus		*M. l. kaguyae*		*M. l.* cf. *kaguyae* (Hokkaido)		*M. l.* cf. *kaguyae* (Kunashir and Sakhalin)		*M. l. eniseensis*	
	n = 15		n = 39		n = 6		n = 4		n = 21	
	min–max	mean ± stddiv	min–max	mean ± stddiv	min–max	mean ± stddiv	min–max	mean ± stddiv	min–max	mean ± stddiv
CBL	12.99–13.71	13.44 ± 0.24	12.75–13.89	13.24 ± 0.27	13.2–13.89	13.42 ± 0.27	13.15–13.43	13.28 ± 0.12	13.08–14.29	13.74 ± 0.32
CCL	12.2–12.89	12.58 ± 0.23	12–13.1	12.47 ± 0.27	12.26–12.96	12.52 ± 0.25	12.34–12.54	12.43 ± 0.08	12.38–13.25	12.88 ± 0.26
OH	5.46–5.92	5.74 ± 0.16	5.4–6.04	5.72 ± 0.14	5.47–5.86	5.72 ± 0.15	5.55–5.82	5.70 ± 0.11	5.52–6.05	5.79 ± 0.15
MW	7.49–8	7.74 ± 0.18	7.38–8.04	7.67 ± 0.17	7.68–7.74	7.72 0.02	7.53–7.71	7.61 ± 0.07	7.57–8.49	7.85 ± 0.20
BCW	7–7.79	7.37 ± 0.22	7.04–7.65	7.30 ± 0.16	7.02–7.39	7.23 ± 0.15	7.06–7.51	7.19 ± 0.22	7.07–7.76	7.45 ± 0.17
POW	3.87–4.39	4.10 ± 0.17	3.76–4.22	3.97 ± 0.11	3.93–4.05	3.98 ± 0.04	3.88–4.06	3.97 ± 0.09	3.86–4.35	4.13 ± 0.13
WR	4.08–4.51	4.27 ± 0.14	4.02–4.58	4.25 ± 0.15	4.11–4.39	4.27 ± 0.10	4.15–4.38	4.26 ± 0.09	4.1–4.58	4.35 ± 0.13
LR	3.4–3.73	3.54 ± 0.09	3.08–3.74	3.40 ± 0.15	3.4–3.69	3.51 ± 0.10	3.41–3.58	3.48 ± 0.07	3.2–3.72	3.56 ± 0.13
CM3	3.37–5.39	5.12 ± 0.50	4.92–5.38	5.16 ± 0.12	5.05–5.3	5.20 ± 0.10	5.09–5.28	5.18 ± 0.10	5.09–5.56	5.31 ± 0.11
P4M3	3.75–4.04	3.90 ± 0.10	3.62–4.09	3.80 ± 0.11	3.67–4.06	3.89 ± 0.14	3.74–3.94	3.84 ± 0.10	3.79–4.05	3.93 ± 0.08
C	0.86–1.02	0.92 ± 0.04	0.79–0.98	0.88 ± 0.04	0.86–0.98	0.91 ± 0.04	0.84–0.89	0.86 ± 0.02	0.83–0.95	0.88 ± 0.03
PD	0.39–0.69	0.52 ± 0.09	0.38–0.74	0.56 ± 0.07	0.4–0.61	0.49 ± 0.08	0.51–0.61	0.55 ± 0.05	0.49–0.76	0.57 ± 0.07
CC	3.85–4.23	4.07 ± 0.11	3.62–4.29	4.08 ± 0.13	4–4.19	4.10 ± 0.07	3.9–4.19	4.02 ± 0.13	3.92–4.32	4.10 ± 0.11
M3M3	5.5–5.97	5.75 ± 0.11	5.31–6	5.74 ± 0.15	5.58–5.86	5.72 ± 0.11	5.65–5.77	5.71 ± 0.06	5.6–5.87	5.71 ± 0.08
WM3	1.31–1.47	1.38 ± 0.05	1.26–1.43	1.37 ± 0.05	1.38–1.49	1.44 ± 0.04	1.26–1.43	1.36 ± 0.07	1.29–1.46	1.38 ± 0.06
LM3	0.64–0.77	0.72 ± 0.03	0.66–0.77	0.71 ± 0.03	0.69–0.8	0.74 ± 0.04	0.68–0.69	0.68 ± 0.00	0.68–0.81	0.73 ± 0.03
WM2	1.36–1.51	1.43 ± 0.05	1.32–1.52	1.42 ± 0.05	1.39–1.55	1.48 ± 0.06	1.37–1.46	1.43 ± 0.04	1.33–1.51	1.41 ± 0.05
LMD	9.84–10.71	10.24 ± 0.20	9.46–10.64	10.12 ± 0.24	10.07–10.57	10.25 ± 0.23	9.82–10.15	10.01 ± 0.15	10.01–10.82	10.47 ± 0.24
LMDa	10.05–11.1	10.62 ± 0.24	9.15–11.05	10.47 ± 0.33	10.44–10.99	10.65 ± 0.22	10.11–10.54	10.36 ± 0.20	10.29–11.27	10.87 ± 0.27
HMD	3.33–3.76	3.52 ± 0.13	3.27–3.72	3.49 ± 0.13	3.42–3.77	3.59 ± 0.12	3.38–3.54	3.48 ± 0.07	3.26–3.73	3.54 ± 0.12
MCM3	5.43–5.89	5.64 ± 0.12	5.25–5.74	5.53 ± 0.12	5.44–5.7	5.54 ± 0.10	5.53–5.63	5.59 ± 0.04	5.48–5.88	5.70 ± 0.13
MPM3	3.93–4.34	4.10 ± 0.12	3.78–4.24	4.00 ± 0.11	3.93–4.17	4.06 ± 0.09	3.95–4.11	4.05 ± 0.07	3.79–4.31	4.13 ± 0.12

The majority of samples (81%) belonged to the E4 or E8 haplotypes, while their ranges overlapped only in one locality (Argaley-3 Cave). The E4 haplotype was widespread in Baikal Region, Transbaikalia, and Northern Mongolia, and the E8 haplotype – at the western edge-of-the range, in the Altai Mountains and the Kuznetsk Alatau Range. The population in Baikal Region and Transbaikalia contained five unique haplotypes.

Morphometric analyses

The minimum, maximum and mean values of cranial and dental measurements are given in Table 2. The morphometric data were quite poorly factorized: the total contribution of the first four Factors to the total variance was less than 70%, which indicated low morphological variability within *M. longicaudatus*.

Nevertheless, in the space of the first two Principal Components, despite the wide overlap of geographic samples, one could observe a tendency to separate at least eastern (*longicaudatus* and *kaguyae*) and western (*eniseensis*) races (Fig. 4). At the same time, animals from Sakhalin and Kunashir were clearly associated with the eastern samples. The first PC was highly correlated with overall skull size, with significant input made by CBL, CCL, mandible length, and lengths of tooth rows; the second PC was most highly correlated with M2W (Table 3).

Geographical samples were better separated by the results of Discriminant Function analysis (Fig. 5). There was also a wide overlap here, but larger parts of the samples representing one or another accepted subspecies were separated. Non-significant differences ($p > 0.1$, Squared Mahalanobis distance between centroids ca. 5.2) were present only between two samples from Honshu. The rest of the samples were significantly divided conditionally ($p < 0.1$). The differences between the sample "Siberia" and all others were the largest among the used training sets (Table 4). The relatively large differences between the sample from Hokkaido and the remaining samples could be an artifact of the small size due to this sample. Despite a distinct trend towards separating the geographic races of *M. longicaudatus*, individual specimens fell deep within the "foreign" samples. For example, a specimen from the Novosibirsk Region was definitely closer to *M. l. longicaudatus* than to *M. l. eniseensis*; in terms of Mahalanobis distances, however, this specimen was far from all samples. The specimen from the Tunkinskie goltsy Range was quite definitely associated with *M. l. eniseensis*, although its distances from all samples were also quite large. Specimens from Transbaikalia (the Shilka River valley) unexpectedly turned out to be similar to animals from Honshu (and in any case belonged to the eastern rather than the western race). The specimen from Sakhalin was almost equidistant from all samples, although it was formally classified more as a western one. The specimens

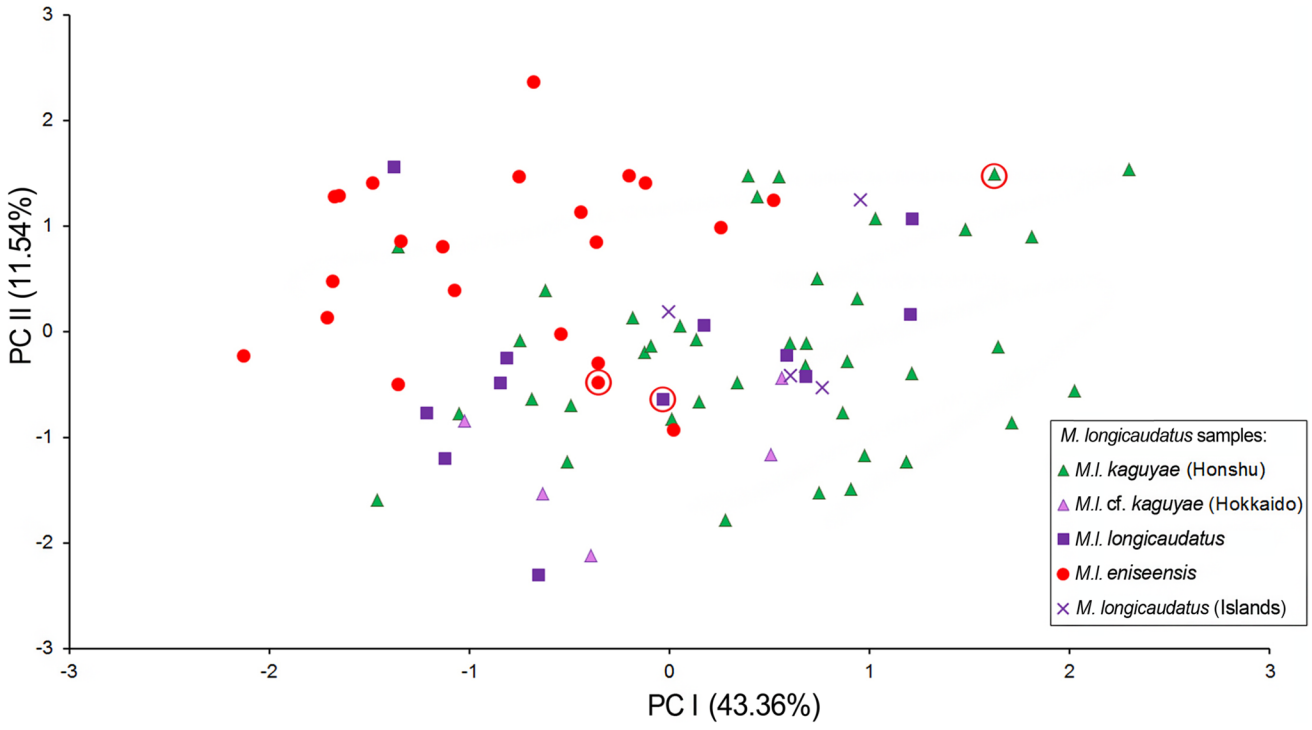

Fig. 4 Bivariate scatter plot for the first two factors of a Principal Component analysis based on 22 cranial and dental measurements of 83 M. *longicaudatus* specimens. The holotypes of three accepted subspecies are marked with red circles

Table 3 Results of PCA applied to 83 specimens of *M. longicaudatus* based on 22 cranial measurements: factor loadings, eigenvalues and percentage of total variance. See text for measurement abbreviations. Loading values above 0.8 by module are highlighted in bold

	Factor 1	Factor 2	Factor 3	Factor 4
CBL	**−0.874**	0.232	0.095	−0.172
CCL	**−0.891**	0.240	−0.023	−0.139
OH	−0.535	−0.024	−0.313	0.018
MW	−0.570	0.236	−0.242	0.495
BCW	−0.616	0.139	−0.387	0.416
POW	−0.632	0.254	−0.491	0.224
WR	−0.6431	−0.051	−0.354	−0.136
LR	−0.715	0.227	0.222	−0.093
CM3	**−0.886**	0.039	0.142	−0.144
P4M3	**−0.783**	−0.298	0.260	0.107
C	−0.367	−0.414	0.063	0.292
PD	−0.127	0.646	−0.191	−0.530
CC	−0.606	−0.358	−0.386	−0.148
M3M3	−0.412	−0.425	−0.486	−0.222
WM3	−0.387	−0.637	0.102	−0.227
LM3	−0.490	−0.320	0.180	−0.011
WM2	−0.324	**−0.768**	−0.069	−0.058
LMD	**−0.902**	0.227	0.130	−0.007
LMDa	**−0.827**	0.262	0.194	0.042
HMD	−0.456	0.059	0.503	0.252
MCM3	**−0.885**	0.061	0.192	−0.122
MPM3	**−0.775**	−0.133	0.237	0.001
Eigenvalue	9.540	2.538	1.694	1.149
% of total variance	43.363	11.538	7.700	5.223
Cumulative variance	43.363	54.901	62.601	67.824

from Kunashir were also not unambiguously associated with any of the samples in terms of distances from their centroids; with Posterior probabilities, they were all formally classified as eastern.

Discussion

The predicted distribution of suitable conditions for *M. l. longicaudatus*, based on SDM, correspond to several ecoregions (Olson et al. 2001). These include Central Korean and Northeast China Plain deciduous forests (Liaoning, Jilin, and Heilongjiang Provinces of China), Ussuri broadleaf and mixed forests, Manchurian mixed forests (mainly Liaoning Province, to a lesser extent Jilin and Heilongjiang Provinces of China, and Amur Region of Russia), and Okhotsk-Manchurian taiga at the northern and northeastern edges of the subspecies range (S Khabarovsk Krai, Russia), as well as Suiphun-Khanka meadows and forest meadows, Amur meadow steppe. In turn, suitable areas from the SDM for *M. l. eniseensis* correspond to such ecoregions as East Siberian taiga, Sayan montane conifer forests, Western Siberian hemiboreal forests, Altai montane forest / forest steppe, South Siberian forest steppe, and Kazakh forest steppe. In this study, we caught *M. l. longicaudatus* and *M. l. kaguyae* in foraging habitats in forests, and *M. l. eniseensis* at the cave entrances in forests (two sites), forest-steppe (one site), steppe (one site), and agricultural grounds (one site).

It can be noted that by the proportions of the skull and teeth, we observe the most obvious differences between the western and eastern *M. longicaudatus* (i.e., between the form *eniseensis* and other analyzed samples). At the same time, apparently, the scale of individual variability is large enough in relation to geographic variability, so that individual samples overlap significantly in all cases. This, perhaps, explains the position of individual specimens, which differs markedly from what was expected.

In general, morphometric and molecular data converge and do not contradict the presence of three subspecies in spite of the overall variability within the species being quite low. The results of the species distribution modeling also converge with the morphometric and molecular data, predicting suitable areas for the western *M. longicaudatus* (*M. l. eniseensis*) to the west of the Greater Khingan, and for the eastern (*M. l. longicaudatus*) to the east of it. The morphological similarity of the specimens from Transbaikalia with the eastern *M. longicaudatus*, which contradicts the molecular data, may be explained by potential hybridization between the two subspecies at the border of their ranges. The status of *M. l. eniseensis* is beyond doubt and its distribution borders are defined, while a border between *M. l. longicaudatus* and *M. l. kaguyae* looks blurred.

Although western and eastern morphological subspecies/forms are known in at least five bat species (*M. longicaudatus*, *M. sibiricus*, *M. petax*, *Murina hilgendorfi*, and *Vespertilio sinensis*) from the temperate zone of the Eastern Palaearctic (Strelkov 1983; Tsytsulina and Strelkov 2001; Kruskop 2004, 2005), paleoclimatic, climatic and topographic patterns of their distribution have not been previously studied. Thus, we showed for the first time that the Greater Khingan Mountains could be treated as distribution boundary for each of the two mainland subspecies of *M. longicaudatus*. The Greater Khingan Mountains stretch from northeast to southwest for 1200 km, its steep eastern slopes incise into the Songliao Plain, and the western slopes gradually transit into the Mongolian Plateau. The eastern slopes of the Greater Khingan Mountains block the summer marine monsoon, thus forming a precipitation contrast between the humid forest biome and the semiarid grassland biome. Cold–temperate coniferous forest cover in the north gradually transits to mid-temperate grassland landscapes in the south (Fu et al. 2018; Zheng et al. 2008).

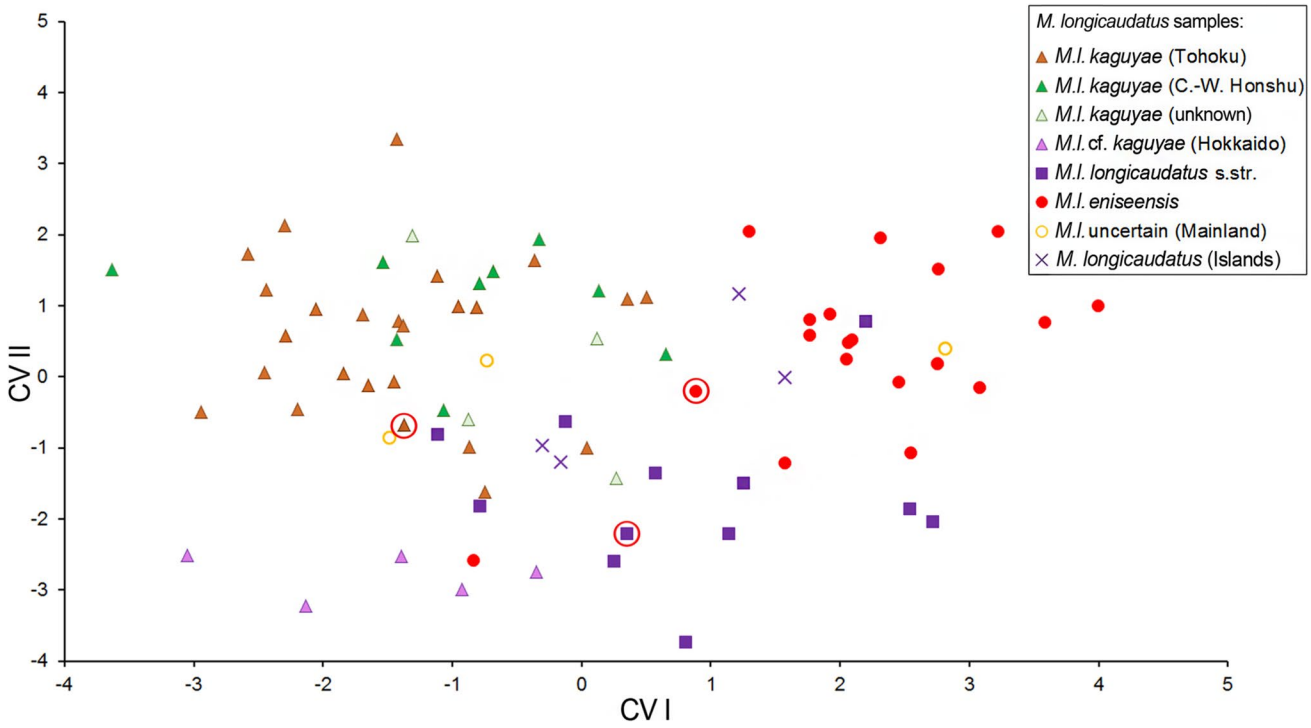

Fig. 5 Bivariate scatter plot for the first and second canonical variables of a Discriminant Function analysis calculated for 22 cranial and dental measurements of 83 M. *longicaudatus* specimens. The holotypes of three accepted subspecies are marked with red circles

Table 4 Significance of difference between training sets of *M. longicaudatus* (*p*-level, below the diagonal) and phenetic distances between them (above diagonal) calculated in forward stepwise Discriminant Function analysis

	N Honshu	C and W Honshu	Hokkaido	Primorye	Siberia
N Honshu		5.15612	16.93690	12.30136	14.77538
C and W Honshu	0.440149		23.23051	13.89140	15.02678
Hokkaido	0.015475	0.010270		19.59050	29.17134
Primorye	0.000876	0.014184	0.017850		11.40104
Siberia	0.000007	0.002213	0.000227	0.004904	

The role of mountains as geographical barriers in the evolutionary history of closely related species, subspecies, and lineages of bats has been quite well studied in the Western Palaearctic. For example, the origin of *M. nattereri helverseni* from the *M. nattereri* species complex associated with isolation in the Italian Peninsula, and *M. escalerai escalerai* with isolation in the Iberian Peninsula, where the barriers were the Alps and the Pyrenees, respectively (Ibáñez et al. 2006; Çoraman et al. 2019). Razgour et al. (2013) showed that the Pyrenees also limit the contemporary gene flow in *P. austriacus*, and all European haplotypes originated from a single Iberian haplotype, when a limited number of individuals crossed this geographical barrier. In the New World, studies based on molecular data and geometric morphometrics have shown the existence of at least four species within the *Glossophaga soricina* species complex (Phyllostomidae), that has been attributed to the most recent Andes uplift (Dias et al. 2017; Calahorra-Oliart et al. 2021).

In turn, mainland and insular morphological subspecies/forms have been also described for five Far East bat species: *M. longicaudatus*, *M. bombinus*, *M. macrodactylus*, *Murina hilgendorfi*, and *M. ussuriensis* (Imaizumi 1956; Yoshiyuki 1989; Tiunov 1997; Kruskop 2005). The origin of these insular forms is associated with isolation in the Japanese archipelago and Sakhalin Island, or only in the Japanese archipelago.

The distribution patterns of other bat species in the temperate zone of the Eastern Palaearctic are still uncertain and insufficiently studied. Thus, it is still unknown whether they correlate with that of *M. longicaudatus* or if different bat species were influenced by different factors during their evolutionary history and colonization of the region. Further comprehensive studies of population structure in the Eastern Palaearctic bat species are needed, based on both genomic (SNP analysis) and morphological data.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s13364-025-00782-5.

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Authors contribution D.V.K. conceived and designed the study. D.V.K., K.K. and U.V.G. caught the bats in the field. D.V.K. performed molecular and data analyses. S.V.K. performed morphometric analyses. A.A.G. performed the species distribution modelling. D.V.K., S.V.K., A.A.G., K.K. and U.V.G. prepared the manuscript.

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Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval All procedures involving animals were in compliance with the European Convention for the Protection of Vertebrate Animals used for Experimental and Other Scientific Purposes (Strasbourg, 18 March 1986), and ethical approval was granted by the University of Tyumen Biomedical Ethic Committee (No. 7, 7 July 2023, Tyumen, Russia). *M. longicaudatus* are listed in *The IUCN Red List of Threatened Species* (2021) as *Least Concern*.

Consent to participate This is not applicable to the present manuscript.

Consent for publication All authors reviewed and approved the final version of the manuscript.

Conflict of interest The authors declare no competing interests.

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