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On the distribution and taxonomy of bats of the *Myotis mystacinus* morphogroup from the Caucasus region (Chiroptera: Vespertilionidae)

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Abstract: Due to the combination of general morphological similarity among representatives of particular populations and/or taxa, the taxonomy of the *Myotis mystacinus* morphogroup is traditionally considered to be one of the most complex topics of bat systematics. We used a combination of genetic and morphological approaches to identify which taxa of the morphogroup inhabit the broader Caucasus region (i.e. the territory between Crimea, Southern Russia, Northern Anatolia, and Northern Iran, incl.) and to define the relationships of these taxa to other Palaearctic populations of the morphogroup. Based on the genetic identification (complete sequence of the cytochrome *b* gene) of 56 specimens of the morphogroup originating from the region and the subsequent morphological comparison of more than 100 museum specimens, five species were shown to occur in the Caucasus region: *Myotis mystacinus* s.str., *M. davidii*, *M. alcathoe*, *M. hyrcanicus*, and *M. brandtii*. While the intraspecific positions of the Caucasian populations of *M. mystacinus* and *M. davidii* remain unresolved, the populations of *M. brandtii* belong to the nominotypical form of this species, and the populations of *M. alcathoe* represent an endemic subspecies, which is here newly described; *M. hyrcanicus* is regarded a monotypic species.

Key words: *Myotis*, mtDNA, cytochrome *b*, morphometrics, identification, taxonomy, Middle East, Palaearctic

1. Introduction

Whiskered bats, or the *Myotis mystacinus* morphogroup, are a group of morphologically very similar bats, including the smallest representatives of the genus *Myotis*. Besides their small body size, these bats are characterised by their dark-coloured face and notched ears, and by the wing membrane attaching the tibia at its distal part. For a long time, only one species was identified within the group, *M. mystacinus* (Kuhl, 1817), considered to be distributed over an extremely large range covering most of the Palaearctic and Oriental regions (Tate, 1941; Ellerman and Morrison-Scott, 1951; Kuzâkin, 1950, 1965). Only recently, more species have started to be recognised within the group, based originally on various morphological traits, and later also on karyological differences and only partially on molecular genetic analyses (cf. Simmons, 2005).

Considering the most recent studies, the *M. mystacinus* morphogroup consists of several forms in the western part of the Palaearctic (Benda and Tsytsulina, 2000; Cyculina, 2000; Tsytsulina, 2000, 2001; von Helversen et al., 2001; Benda and Karataş, 2005). As noted above, the group was initially considered monospecific but polymorphic with a large number of subspecies. In the 1960s, the East European subspecies *brandtii* was found in sympatry with the nominotypical form of *M. mystacinus* and its species status was further supported by morphological differences evidenced throughout the European populations (Topál, 1958; Hanák, 1965, 1970; Gauckler and Kraus, 1970); for details on this history, see Benda (1999) and Benda and Tsytsulina (2000). However, in the same period, Stubbe and Chotolchu (1968) recognised three morphotypes in the rank of *M. mystacinus* in the Palaearctic. Besides the *mystacinus*- and *brandtii*-morphotypes, suggested as full species also by other authors (see above), they reported the *przewalskii*-morphotype (a taxon described from the East Turkestan plateau of China; Bobrinskoj, 1926). The latter form was later found in South-Eastern Europe and in Asia Minor (Stubbe and Chotolchu, 1968; von Helversen, 1989a, 1989b). Additionally, Volleth (1987) found four distinct karyotype forms of the group in Europe and Turkey, *M. mystacinus*, *M. brandtii*, and two others, named provisionally *Myotis* sp. A and *Myotis* sp. B.

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Previous revisions of the group (Strelkov and Buntova, 1982; Strelkov, 1983a, 1983b) revealed only two species in the Palaearctic: the almost invariable *M. brandtii* and the highly variable *M. mystacinus*, in which four subspecies were recognised (*mystacinus*, *popovi*, *aurascens*, *przewalskii*). Subsequent comparison by Benda and Tsytsulina (2000) demonstrated an existence of several morphotypes in the Western Palaearctic, some of which were found to occur in sympatry, mainly in the Eastern Mediterranean region and Southern Russia. Based on these findings, the authors suggested the existence of the following taxa in the region: *Myotis brandtii* (Eversmann, 1845) (incl. *sibiricus* Kaŝenko, 1905, *gracilis* Ognev, 1927, *coluotus* Kostroň, 1943; Palaearctic forests from Western Europe to the Far East), *M. mystacinus* (Kuhl, 1817) (incl. *nigricans* Fatio, 1869, *lugubris* Fatio, 1869, *occidentalis* Benda, 2000, *caucasicus* Tsytsulina, 2000; European mixed forests from Morocco to the Ural Mts. incl. the Mediterranean), *M. aurascens* Kuzâkin, 1935 (incl. *bulgaricus* Heinrich, 1936, *popovi* Strelkov 1983, *Myotis* sp. A sensu Volleth, 1987, and *przewalskii* sensu von Helversen, 1989a, 1989b; Palaearctic forest-steppes from the Central Mediterranean to Eastern Europe and Mongolia, incl. the Middle East, possibly also Central Asia), *M. hajastanicus* Argiropulo, 1939 (Sevan Lake Basin, Armenia), and *M. nipalensis* (Dobson, 1871) (incl. *przewalskii* Bobrinskoj, 1926, *meinertzhageni* Thomas, 1926, *transcaspicus* Ogneff & Heptner, 1928, *kukunorensis* Bobrinskoj, 1929, *sogdianus* Kuzâkin, 1934, *pamirensis* Kuzâkin, 1935; arid zones of the Southern Palaearctic from the Middle East to Central Asia).

However, Mayer and von Helversen (2001) showed genetic similarity between the forms *mystacinus* and *przewalskii* (sensu von Helversen, 1989a), *mystacinus* and *Myotis* sp. A (sensu Volleth, 1987), and *mystacinus* and *aurascens* (sensu Benda and Tsytsulina, 2000), respectively. At the same time, Mayer and von Helversen (2001) pointed out the genetic differences between the *mystacinus/aurascens/nipalensis/przewalskii* clade and another form, which was named *M. ikonnikovi* by von Helversen (1989a), although this name belongs in fact to another East Palaearctic species, and *Myotis* sp. B by Volleth (1987). This newly separated form was described as a new species, *M. alcathoe* von Helversen & Heller, 2001 (von Helversen et al., 2001). This species was subsequently confirmed to occur in almost the whole of Southern and Central Europe and its northern margin of distribution was identified to pass from Great Britain through Germany and Poland to Western Ukraine and Romania (Ruedi et al., 2002; Benda et al., 2003; Agirre-Mendi et al., 2004; Schunger et al., 2004; Stadelmann et al., 2004; Jére and Dóczy, 2007; Niermann et al., 2007; Spitzeneberger et al., 2008; Lučan et al., 2009; Bashta et al., 2010; Danko et al., 2010; Jan et al., 2010; etc.).

Thus, four forms of the *Myotis mystacinus* morphogroup are reported to occur in the western half of Europe (including the Balkans and Western Ukraine), exactly as was suggested by the karyological investigations by Volleth (1987) and empirical field observations by von Helversen (1989a), namely *M. mystacinus*, *M. brandtii*, *M. aurascens*, and *M. alcathoe* (see Benda and Karataş, 2005; Dietz et al., 2007; Dietz and Kiefer, 2014).

The situation of the *Myotis mystacinus* morphogroup in the Caucasus region was first examined in detail by Strelkov and Buntova (1982) and Strelkov (1983a), although preliminary comparisons were made previously by Kuzâkin (1935) and Argiropulo (1939). Strelkov (1983a) found two species in the area, *M. mystacinus* and *M. brandtii*, similarly as in the whole Palaearctic (see above). Based on a thorough examination of cranial and dental characters, Benda and Tsytsulina (2000) and Cyculina (2000) demonstrated the existence of five morphotypes in the region, *Myotis brandtii*, *M. mystacinus caucasicus* Tsytsulina, 2000 (newly described), *M. aurascens*, *M. hajastanicus*, and *M. nipalensis*. While *M. brandtii* was reported to occur in the forested north-western part of the region only, *M. nipalensis* in the rather arid south-eastern part of the region, and *M. hajastanicus* as an endemic of the Sevan Lake Basin (Armenia), the two remaining forms were considered widespread in the region (see Benda and Tsytsulina, 2000: 357, Fig. 45).

Later on, based on an examination of external characters, Gazarân (2009) showed the existence of three distinct forms in the north-western part of the Caucasus (Russia and Abkhazia), which he named *M. brandtii*, *M.* cf. *aurascens*, and *M.* cf. *alcathoe*, considering their external similarity with the European forms (cf. Dietz et al., 2007). This corresponds well with the findings by Benda and Tsytsulina (2000) and Cyculina (2000) from the respective area, who suggested the occurrence of *M. brandtii*, *M. aurascens*, and *M. mystacinus caucasicus* there. While Benda and Tsytsulina (2000) and Cyculina (2000) compared an extensive number of museum specimens of the morphogroup from the whole South-Western Palaearctic, from the respective part of the Caucasus region they examined limited material. Hence, Gazarân's (2009) approach could indicate an original and more profound view due to the more extensive material examined as well as due to the consideration of the new findings on the taxonomy of the group since 2000 (see von Helversen et al., 2001; Benda and Karataş, 2005; etc.).

Recently, Tsytsulina et al. (2012) performed a geographically very broadly sampled comparison of the morphogroup based on two mitochondrial markers. They found four separate lineages in the Western Palaearctic, which they coidentified with *M. mystacinus*, *M. brandtii*, and *M. alcathoe* from Europe and *M. aurascens* from a very

broad area between Southern Europe and Korea. Thus, this analysis did not prove a separate existence of one form recognised by Benda and Tsytsulina (2000) as *M. nipalensis*. Tsytsulina et al. (2012) included the respective samples under the broadly distributed *M. aurascens*, although it represents a junior synonym among the names applicable to the respective lineage (see Benda and Tsytsulina, 2000; Benda and Karataş, 2005). This lineage was the only taxon of the morphogroup proved by this molecular genetic analysis (and its limited sampling, respectively) from the broadly considered Caucasus region.

Benda et al. (2012) briefly analysed some specimens of the morphogroup coming from Iran, both morphologically and genetically. They found three separate morphotypes there, each of them belonging to a separate genetic lineage. Two of them were coidentified by the latter authors with the existing taxa *M. mystacinus* and *M. davidii* (a prior name in the lineage of *nipalensis*, *aurascens*, and *transcaspicus*; see also Benda and Karataş, 2005), while the third form, a lineage of its own closely positioned by its genetic and morphological traits to the European *M. alcathoe*, was described as a new species, *M. hyrcanicus* Benda, Reiter & Vallo, 2012.

The findings and opinions summed up above indicate that the broader Caucasus region (i.e. the territory between Crimea, Southern Russia, Anatolia, and Northern Iran, incl.) may harbour a much higher diversity of the *M. mystacinus* morphogroup than any other area of the Palaearctic. Thus, the aim of this study was to answer the questions arising from the presented taxonomic opinions concerning the Caucasian populations of the *Myotis mystacinus* morphogroup and to revise the currently valid scheme of the group systematics. The main tasks were: 1) to determine how many taxa of the morphogroup inhabit the Caucasus region, 2) to understand their relationships to other Palaearctic populations, and 3) to assess the taxonomic implications of these findings. To cope with these tasks, we examined as much material from the Caucasus region as possible using both morphological and genetic approaches. We employed a slightly different methodological approach than that applied in previous studies. Since morphological analysis was shown not to be a sufficient approach to identify particular evolutionary entities, we first used an analysis of a mitochondrial marker to sort separate lineages present in the Caucasus region. Based on the specimens selected by this first step, we finally identified the morphotypes in the available museum material, including the type specimens of all respective names, and defined the morphological, taxonomic, and geographical content of the particular evolutionary units within the *M. mystacinus* morphogroup in the broader Caucasus region.

2. Materials and methods

2.1. Genetic analysis

We analysed the mitochondrial DNA in a set of whiskered bats from the Caucasus and neighbouring areas of the Western Palaearctic as listed in Appendix 1. The genetic material was obtained from pectoral muscles or wing punches preserved in alcohol. Total genomic DNA was extracted from with the JetQuick Spin Tissue Kit (Genomed, Löhne, Germany) or Genomic DNA Mini Kit (Geneaid, New Taipei City, Taiwan) according to the manufacturers' protocols. The complete mitochondrial gene for cytochrome *b* (cyt *b*) was amplified via PCR using primer pairs F1 (modified; 5'-CCACGACCAATGACAYGAAAA-3') and R1 (5'-CCTTTTCTGGTTTACAAGACCAG-3') by Sakai et al. (2003) in a reaction volume of 25 µL containing 12.5 µL of Combi PPP Master Mix (Top-Bio, Prague, Czech Republic), 200 µM of each primer, and 2.5 µL of extracted DNA. Initial denaturation at 94 °C for 3 min was followed by 35 cycles of denaturation for 40 s at 94 °C, annealing for 40 s at 50 °C, and extension for 90 s at 65 °C, with final extension at 65 °C for 5 min. PCR products were inspected by electrophoresis on 2% agarose gel with a nucleic acid stain. The resulting PCR products were purified with the JetQuick PCR Purification Kit (Genomed) or Gel/PCR DNA Fragments Extraction Kit (Geneaid) and sequenced commercially at Macrogen Inc. (Seoul, Korea) using BigDye Terminator sequencing chemistry (Applied Biosystems, Foster City, CA, USA) on an ABI 3730xl sequencer. Primers for sequencing cyt *b* were the same as for PCR amplification, or, where needed, a newly designed internal *Myotis*-specific primer mau_iF496 (5'-TCTCGTAGARTGAATTTGAG-3') was used to obtain clear readings for the 3' half of the PCR product.

Sequences were assembled and edited in Sequencher 4.7 (Gene Codes, Ann Arbor, MI, USA) and the Contig Assembly Program (CAP; Huang 1992) implemented in BioEdit 7.0 (Hall, 1999). All new sequences were submitted to GenBank with accession numbers KU060252–KU060282. For comparison, GenBank sequences of *Nyctalus leisleri* (Kuhl, 1817), *N. noctula* (Schreber, 1774), and *Vespertilio murinus* Linnaeus, 1758 (GenBank accession numbers JX570901, JX570902, and AF376834, respectively) were included as an outgroup for rooting trees. Phylogenetic reconstructions were done under the Bayesian approach using MrBayes 3.2 (Ronquist and Huelsenbeck, 2003). Two independent runs of 1,000,000 generations were carried out under the GTR+Γ+I substitution model, with the first 25% of sampled parameters and trees discarded as burn-in. Genetic divergences were expressed as pairwise uncorrected p-distances.

2.2. Morphological analysis

The museum material of the *Myotis mystacinus* morphogroup from the Caucasus region in its broader sense, including

Crimea, Turkey, and NW Iran, as well as the comparative material from the adjacent areas of the Western Palaearctic used in the morphological analyses, is listed in Appendix 2. The comparative material included most of the respective type specimens/series concerning the morphogroup (*alcathoe* von Helversen & Heller, 2001; *aurascens* Kuzâkin, 1935; *caucasicus* Tsytsulina, 2000; *hajastanicus* Argiropulo, 1939; *hyrcanicus* Benda, Reiter & Vallo, 2012; *meinertzhageni* Thomas, 1926; *pamirensis* Kuzâkin, 1935; *popovi* Strelkov, 1983; *sogdianus* Kuzâkin, 1934; and *transcaspicus* Ogneff & Heptner, 1928). For morphometric analyses, we primarily used skull, teeth, and selected external metric data; for the dimensions evaluated see Section 2.3 below. The specimens were measured in a standard way using mechanical or optical callipers. Skull and dental measurements were taken according to Benda and Tsytsulina (2000); the dental measurements were taken including cingula of the respective teeth. Descriptive statistics of each group and multivariate analyses of morphometric data were performed using the Statistica 6.0 software. Factor analyses (PCA) of skull and tooth metric and phenetic data were used to determine particular genetically verified morphotypes within the material that was examined with the help of the molecular genetic analysis.

The term 'Province' is used for all first-level administrative units of the respective countries (instead of the terms Republic, Oblast', Kraj, Region, Vilayet, Ostan, etc.), and the term 'District' is used for all second-level divisions.

2.3. Abbreviations

2.3.1. Dimensions

External dimensions: LAt – forearm length; LPol – thumb length; LTib – tibia length.

Cranial dimensions: LCr – greatest skull length; LCb – condylobasal length; LaZ – zygomatic width; LaI – interorbital width; LaInf – infraorbital width; LaN – neurocranium width; AN – neurocranium height; CC – rostral width across upper canines (incl.); M^3M^3 – rostral width across third upper molars (incl.); I^1M^3 – length of upper tooth-row between first incisor and third molar (incl.); CM^3 – length of upper tooth-row between canine and third molar (incl.); P^4M^3 – length of upper tooth-row between third premolar and third molar (incl.); M^1M^3 – length of upper tooth-row between first and third molars (incl.); M^1M^2 – length of upper tooth-row between first and second molars (incl.); CP^4 – length of upper tooth-row between canine and third premolar (incl.); P^2P^3 – length of upper tooth-row between first and second premolar (incl.); LMd – mandible length; ACo – coronoid height of mandible; I_1M_3 – length of lower tooth-row between first incisor and third molar (incl.); CM_3 – length of lower tooth-row between canine and third molar (incl.); P_4M_3 – length of lower tooth-row between third premolar and third molar (incl.); M_1M_3 – length of lower tooth-row between first and third molars (incl.); CP_4 – length of lower tooth-row between canine and third premolar (incl.); P_2P_3 – length of lower tooth-row between first and second premolar (incl.).

Dental dimensions: LCn – mesiodistal crown length of upper canine; LaCn – palatolabial crown width of upper canine; P^3 – mesiodistal crown length of second upper premolar; P_3 – mesiodistal crown length of second lower premolar; ACin – height of the cingular cusp on the third upper premolar; P^4 – palatolabial crown width of fourth upper premolar; M^1 – palatolabial crown width of first upper molar; M^2 – palatolabial crown width of second upper molar; M^3 – palatolabial crown width of third upper molar.

Phenetic characters: CnR – canine ratio (relative width of the upper canine crown; LCn/LaCn); MR – molar ratio (relative massiveness of the upper molar crowns; pcl+plph+mcl+mlph); P^3pos – position of the second upper molar within the tooth-row in a five-grade scale: 1 = within the axis of the tooth-row, 5 = completely out of axis in the palatal direction, the first and third premolars mesiodistally in contact); pcl – paraconule massiveness in the first and second upper molars; plph – paraloph massiveness in the first and second upper molars; mcl – metaconule massiveness in the first and second upper molars; mlph – metaloph massiveness in the first and second upper molars; the latter four characters were identified on a three-grade scale: 0 – 0.5 – 1 (for details see Benda and Tsytsulina, 2000).

2.3.2. Others

Collections: BMNH – Natural History Museum, London, United Kingdom; HMNH – Hungarian Museum of Natural History, Budapest, Hungary; MHNG – Natural History Museum, Geneva, Switzerland; NMP – National Museum (Natural History), Prague, Czech Republic; NMW – Natural History Museum, Vienna, Austria; OHC – Otto von Helversen Collection, Erlangen, Germany; SMMZ – South Moravian Museum, Znojmo, Czech Republic; ZDNU – Zoological Department, Niğde University, Niğde, Turkey; ZIN – Zoological Museum, Russian Academy of Sciences, Saint Petersburg, Russia; ZMB – Zoological Museum, Humboldt University, Berlin, Germany; ZMMU – Zoological Museum, Moscow State University, Moscow, Russia; ZMSO – Zoological Museum, Siberian Branch of the Russian Academy of Sciences, Novosibirsk, Russia.

Specimen data: A – alcoholic preparation; B – stuffed skin (balg); ind. – individual of the sex unidentified; S – skull; Sk – skeleton.

Statistics: df – degrees of freedom; F – F value of ANOVA; M – mean; max., min. – dimension range margins; P – probability; SD – standard deviation.

3. Results

3.1. Genetic analysis

We obtained 92 cyt *b* sequences from specimens of the *Myotis mystacinus* morphogroup (including 56 sequences from specimens originating from the Caucasus region), which were represented by 31 haplotypes, 17 of them obtained (exclusively or in part) from the Caucasian specimens. The phylogenetic analysis consistently divided these haplotypes into six distinct lineages labelled I–VI in the depicted phylogenetic tree (Figure 1), grouped into three main clades (labelled A–C).

A rather low variation was detected within lineages (Table 1), with marked distinctions only between two sublineages of the lineage I (≤4.2%) and between two sublineages of the lineage III (≤2.9%).

A deep split (genetic distance of 14.1%–17.1%) divided the haplotypes into two main groups of clade A (with lineages I and II) and clades B+C (with lineages III–VI), respectively. However, the positions of clades B+C were not resolved within the latter group and therefore this group represented two independent clades (separated by 14.7%–17.0% genetic distance) rather than a single evolutionary unit.

Clade A comprised two deeply split lineages (I+II), with a distance of 12.1%–13.9% between them (Table 1), composed of haplotypes from *M. mystacinus* (I) and *M. davidii* (II; in the sense of Benda et al., 2012, or *M.* cf. *aurascens* in the sense of Gazarân, 2009, respectively). Lineage I comprised eight haplotypes of *M. mystacinus* (five of them from the Caucasus region), arranged into two sublineages (Ia+Ib), separated by a distance of 3.6%–4.2% from each other. Five haplotypes of the Ia sublineage came from 16 specimens originating from the Greater Caucasus of Russia (Krasnodar, Adygea, and Dagestan Provinces;

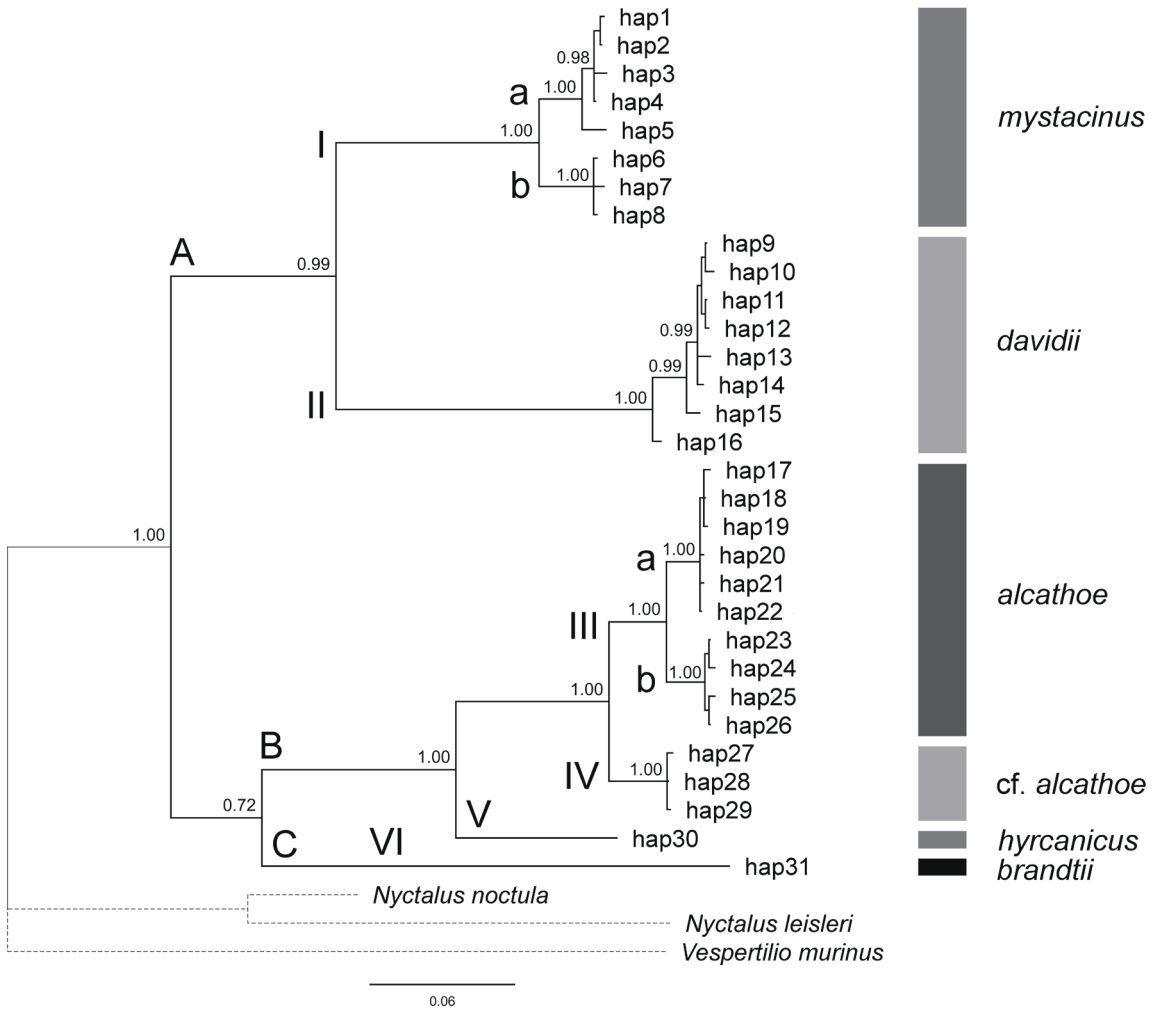

Figure 1. Bayesian 50% majority rule consensus tree depicting the phylogenetic relationships in the *Myotis mystacinus* morphogroup from the Caucasus region and adjacent parts of the Western Palaearctic based on the cytochrome *b* sequences.

Table 1. Uncorrected distances among 31 haplotypes of the cytochrome *b* gene found in the bats of the *Myotis mystacinus* morphogroup from the Caucasus region.

	hap1	hap2	hap3	hap4	hap5	hap6	hap7	hap8	hap9	hap10	hap11	hap12	hap13	hap14	hap15	hap16	hap17	hap18	hap19	hap20	hap21	hap22	hap23	hap24	hap25	hap26	hap27	hap28	hap29	hap30
hap2	0.001	–																												
hap3	0.007	0.006	–																											
hap4	0.003	0.002	0.004	–																										
hap5	0.015	0.014	0.017	0.012	–																									
hap6	0.039	0.038	0.039	0.036	0.039	–																								
hap7	0.041	0.040	0.041	0.039	0.042	0.004	–																							
hap8	0.039	0.038	0.039	0.036	0.039	0.002	0.004	–																						
hap9	0.127	0.126	0.131	0.128	0.132	0.133	0.136	0.135	–																					
hap10	0.127	0.126	0.131	0.128	0.132	0.133	0.136	0.135	0.003	–																				
hap11	0.125	0.125	0.129	0.126	0.130	0.132	0.135	0.134	0.002	0.004	–																			
hap12	0.126	0.125	0.130	0.127	0.131	0.133	0.136	0.135	0.003	0.005	0.001	–																		
hap13	0.129	0.128	0.132	0.130	0.133	0.136	0.139	0.138	0.006	0.009	0.006	0.007	–																	
hap14	0.127	0.126	0.131	0.128	0.130	0.131	0.133	0.132	0.004	0.006	0.004	0.004	0.006	–																
hap15	0.128	0.127	0.132	0.129	0.132	0.135	0.138	0.137	0.010	0.012	0.010	0.011	0.012	0.010	–															
hap16	0.122	0.121	0.125	0.123	0.125	0.127	0.130	0.129	0.019	0.022	0.019	0.020	0.020	0.019	0.018	–														
hap17	0.145	0.144	0.146	0.146	0.146	0.146	0.143	0.146	0.158	0.157	0.156	0.157	0.160	0.156	0.158	0.159	–													
hap18	0.145	0.144	0.146	0.146	0.146	0.146	0.143	0.146	0.158	0.157	0.156	0.157	0.160	0.156	0.158	0.161	0.002	–												
hap19	0.146	0.145	0.147	0.146	0.147	0.146	0.144	0.146	0.159	0.158	0.157	0.158	0.161	0.157	0.159	0.161	0.003	0.001	–											
hap20	0.143	0.142	0.145	0.144	0.145	0.144	0.141	0.144	0.156	0.155	0.154	0.155	0.158	0.154	0.156	0.159	0.004	0.002	0.003	–										
hap21	0.145	0.144	0.146	0.146	0.146	0.146	0.143	0.146	0.158	0.157	0.156	0.157	0.160	0.156	0.158	0.161	0.004	0.002	0.003	0.002	–									
hap22	0.144	0.143	0.146	0.145	0.146	0.145	0.142	0.145	0.157	0.156	0.155	0.156	0.159	0.155	0.157	0.160	0.003	0.001	0.002	0.001	0.001	–								
hap23	0.151	0.150	0.153	0.152	0.151	0.145	0.142	0.145	0.161	0.160	0.159	0.160	0.161	0.159	0.161	0.160	0.027	0.025	0.026	0.025	0.025	0.025	–							
hap24	0.153	0.152	0.154	0.154	0.153	0.146	0.144	0.146	0.162	0.161	0.161	0.161	0.162	0.161	0.162	0.161	0.029	0.027	0.026	0.027	0.027	0.026	0.002	–						
hap25	0.153	0.152	0.154	0.154	0.153	0.146	0.144	0.146	0.163	0.162	0.161	0.162	0.163	0.161	0.163	0.162	0.029	0.027	0.028	0.027	0.027	0.026	0.004	0.005	–					
hap26	0.153	0.152	0.154	0.154	0.153	0.146	0.144	0.146	0.162	0.161	0.161	0.161	0.162	0.161	0.162	0.161	0.027	0.025	0.026	0.025	0.025	0.025	0.002	0.004	0.002	–				
hap27	0.151	0.150	0.153	0.150	0.149	0.146	0.147	0.146	0.161	0.161	0.159	0.160	0.161	0.159	0.161	0.158	0.049	0.049	0.050	0.049	0.049	0.048	0.050	0.052	0.052	0.050	–			
hap28	0.149	0.148	0.151	0.148	0.147	0.145	0.146	0.145	0.159	0.160	0.157	0.158	0.159	0.157	0.161	0.156	0.047	0.047	0.048	0.047	0.047	0.046	0.048	0.050	0.050	0.048	0.002	–		
hap29	0.150	0.149	0.152	0.149	0.148	0.146	0.146	0.146	0.160	0.161	0.158	0.159	0.160	0.158	0.161	0.157	0.048	0.048	0.048	0.048	0.048	0.047	0.049	0.050	0.051	0.049	0.003	0.001	–	
hap30	0.152	0.153	0.157	0.154	0.154	0.144	0.143	0.144	0.158	0.159	0.158	0.157	0.158	0.156	0.157	0.154	0.104	0.103	0.104	0.103	0.101	0.102	0.099	0.101	0.101	0.101	0.097	0.096	0.097	–
hap31	0.167	0.166	0.165	0.166	0.164	0.159	0.161	0.157	0.168	0.169	0.168	0.168	0.166	0.168	0.171	0.164	0.169	0.169	0.170	0.169	0.168	0.168	0.161	0.163	0.163	0.163	0.161	0.159	0.160	0.147

haplotypes 1 and 2) and Central and South-Eastern Europe (Czech Republic, Montenegro, Bulgaria, Greece; haplotypes 3–5). Haplotype 4 of the latter group was obtained from specimens of the *mystacinus* morphotype from the Czech Republic and also from specimens of the *aurascens* morphotype (in the sense of Benda and Tsytsulina, 2000) from the Balkans. Three haplotypes of the Ib sublineage (6–8) come from the south-eastern part of the Caucasus region (N Azerbaijan and NW Iran). The lineage II consisted of eight haplotypes (9–16) of *M. davidii* obtained from 23 specimens originating from the Caucasus region, i.e. from Crimea, Azerbaijan, NW Iran, and various parts of the Greater Caucasus of Russia (Adygea, Krasnodar, and Stavropol' Provinces). Within this lineage, haplotype 16, coming from two specimens collected in NW Iran, showed a slightly separated position from the rest of the haplotypes, representing a distance of 1.8%–2.2%.

Clade B was composed of three lineages, III–V, with distances of 4.6%–10.4% between them (Table 1). Lineage V was situated in the basal position and separated from the two remaining lineages, III and IV, concerning the mutual genetic distances (9.6%–10.4%); it included a single haplotype, haplotype 30, obtained from the holotype of the recently described *M. hyrcanicus* from Golestan Province of Northern Iran (Benda et al., 2012). Lineages III and IV were separated only by 4.6%–5.2% from each other (Table 1). Lineage III consisted of ten haplotypes (17–26) from 27 specimens of *M. alcathoe* from Europe. This lineage was composed of two sublineages (IIIa+IIIb), separated by a distance of 2.5%–2.9% from each other. Sublineage IIIa comprised six haplotypes (17–22), originating from 20 specimens from the Czech Republic, Slovakia, Trans-Carpathian Ukraine, Montenegro, and Bulgaria. Sublineage IIIb comprised four haplotypes obtained from six specimens coming from the Czech Republic, Slovakia, and Bulgaria. Lineage IV was composed of three haplotypes from 19 individuals of *M.* cf. *alcathoe* (sensu Gazarân, 2009) from the western part of the Greater Caucasus of Russia.

Clade C was represented by a single lineage, VI and a single haplotype, 31. This haplotype was obtained from four specimens of *M. brandtii*, originating from very distant locations of the Western Palaearctic, situated in the Greater Caucasus, Crimea, NW Russia (vicinity of St. Petersburg), and Montenegro.

In summary, the haplotypes obtained from the specimens of the *M. mystacinus* morphogroup sampled in the Caucasus region belonged to five well-defined lineages (I, II, IV, V, VI) and these lineages were separated by relatively high genetic distances (>9.5%). Two of these lineages contained a mixture of specimens/haplotypes coming from the Caucasus region and Europe (I, VI), and other lineages (II, IV, V) were represented by unique haplotypes coming solely from the Caucasus region. Four lineages (I, II, IV, VI) were indicated to occur in sympatry in the western part of the Greater Caucasus of Russia.

3.2. Morphological characters

The genetic analysis grouped the specimens of the *M. mystacinus* morphogroup from the Caucasus region into five lineages (see above) and these groups represented at least four distinct morphotypes. Two most peculiar morphotypes were indicated by lineages VI (*M. brandtii*) and IV+V (*M. hyrcanicus* and *M.* cf. *alcathoe*), while bats of lineages I and II (*M. mystacinus* and *M. davidii*) were more similar to each other and their body and skull sizes and particular characters broadly overlapped (Tables 1 and 2; Figures 2 and 3).

Bats of lineage VI, *M. brandtii*, were well separated by all analyses of skull and dental characters from all other specimens, and thus specimens that were not identified with the help of genetic comparison were also used for the analysis and description of morphological traits. These bats were large (LAt 34.4–35.7 mm, LCr 13.7–14.6 mm), with long thumbs (5.2–5.9 mm) and tibiae (15.6 mm). Their skulls showed a relatively low (ANc/LCr 0.32–0.35, ANc/LaN 0.66–0.72) and broad (LaN/LCr 0.48–0.51) braincase, relatively low coronoid processes of the mandible (ACo/LMd 0.26–0.29), relatively narrow rostrum (CC/CM^3 0.62–0.67), and relatively long upper unicuspidal tooth-rows, C–P^4 (CP^4/M^{1}M^3 0.76–0.89). These bats possessed massive molariform teeth (MR 2–4) and large premolars (P^{2}P^3 0.71–0.92 mm, P^3/LCn 0.38–0.51, P$_3$ 0.36–0.47 mm, P^{2}P^3/LCr 0.055–0.064), relatively small third upper molars (M^3/M^1 0.94–1.08), second upper premolars (P^3) positioned exclusively in the axis of the tooth-row (mean P^{3}pos 1.0), third upper premolars (P^4) bearing a high cingular cusp (ACin 0.20–0.31 mm), and mesiodistally very short upper canines (LCn/CM^3 0.14–0.17), their crowns being almost rounded (CnR 1.18–1.30).

Bats of lineages IV and V, i.e. *M. hyrcanicus* and *M.* cf. *alcathoe*, represented a common morphotype that was also well separated by the morphological analyses from the other specimens, but not from each other. These bats were small (LAt 30.1–34.2 mm, LCr 12.5–13.2 mm), with short thumbs (4.1–4.6 mm) and tibiae (12.3–15.3 mm). Their skulls showed a relatively high (ANc/LCr 0.34–0.38, ANc/LaN 0.70–0.77) and narrow (LaN/LCr 0.47–0.50) braincase, relatively high coronoid processes of the mandible (ACo/LMd 0.28–0.31), relatively narrow rostrum (CC/CM^3 0.62–0.68), and relatively short upper unicuspidal tooth-rows, C–P^4 (CP^4/M^{1}M^3 0.67–0.85). These bats possessed rather heavily built molariform teeth (MR 0.5–3.0) and large premolars (P^{2}P^3 0.59–0.77 mm, P^3/LCn 0.34–0.48, P$_3$ 0.29–0.43 mm, P^{2}P^3/LCr 0.046–0.061), relatively large third upper molars (M^3/M^1 0.94–1.16),

Table 2. External, skull, and tooth dimensions (in millimetres) of the examined sample sets of the *Myotis mystacinus* morphogroup from the Caucasus region. See Section 2.3 for explanation of the dimension acronyms.

	Lineage I					Lineage II					Lineage IV					Lineage V	Lineage VI				
	M. mystacinus s.str.					*M. davidii*					*M.* cf. *alcathoe*					*M. hyrcanicus*	*M. brandtii*				
	n	**M**	min	max	SD	n	**M**	min	max	SD	n	**M**	min	max	SD		n	**M**	min	max	SD
LAt	7	**34.94**	34.40	36.10	0.648	12	**34.98**	33.4	37.2	1.012	17	**32.34**	30.1	34.2	0.941	32.4	5	**35.16**	34.4	35.7	0.503
LPol	7	**5.09**	4.70	5.40	0.279	12	**5.83**	5.2	6.3	0.345	17	**4.29**	4.1	4.6	0.145	4.4	4	**5.45**	5.2	5.9	0.311
LTib	7	**16.30**	15.60	16.90	0.465	12	**16.73**	15.9	17.9	0.508	17	**14.17**	12.3	15.3	0.699	14.1	1	15.6			
LCr	7	**13.56**	13.16	14.37	0.439	12	**13.86**	13.42	14.56	0.331	17	**12.88**	12.48	13.22	0.227	12.66	13	**14.06**	13.66	14.57	0.276
LCb	7	**12.97**	12.52	13.71	0.428	12	**13.11**	12.72	13.73	0.296	17	**12.30**	11.84	12.74	0.267	12.06	13	**13.44**	12.92	14.03	0.295
LaZ	6	**8.24**	7.96	8.42	0.166	9	**8.62**	8.22	8.99	0.239	14	**7.93**	7.61	8.23	0.184	8.08	12	**8.50**	8.20	8.81	0.181
LaI	7	**3.40**	3.28	3.65	0.139	12	**3.47**	3.33	3.87	0.140	17	**3.16**	2.87	3.43	0.142	3.27	13	**3.61**	3.40	3.74	0.106
LaInf	7	**3.25**	2.96	3.53	0.176	12	**3.39**	3.13	3.58	0.131	17	**3.21**	3.01	3.42	0.116	3.13	13	**3.52**	3.38	3.67	0.081
LaN	7	**6.60**	6.28	6.93	0.242	12	**6.81**	6.52	7.27	0.219	17	**6.25**	5.94	6.50	0.138	6.14	13	**6.89**	6.66	7.14	0.120
AN	7	**4.79**	4.59	5.07	0.184	12	**4.87**	4.62	5.13	0.156	17	**4.59**	4.44	4.74	0.106	4.52	13	**4.73**	4.52	4.96	0.150
CC	6	**3.33**	3.17	3.57	0.148	12	**3.46**	3.20	3.62	0.138	17	**3.18**	3.05	3.33	0.087	3.27	13	**3.39**	3.27	3.62	0.095
M^3M^3	6	**5.34**	5.09	5.49	0.140	12	**5.43**	5.12	5.74	0.163	16	**5.14**	4.91	5.34	0.102	5.18	13	**5.34**	5.08	5.76	0.174
IM^3	7	**6.28**	6.06	6.68	0.228	12	**6.13**	5.97	6.29	0.096	17	**5.90**	5.58	6.18	0.147	6.01	12	**6.47**	6.23	6.91	0.198
CM^3	7	**5.24**	5.06	5.68	0.233	12	**5.08**	4.96	5.23	0.092	17	**4.89**	4.67	5.11	0.107	4.92	13	**5.29**	5.08	5.71	0.171
P^4M^3	7	**3.90**	3.68	4.16	0.152	12	**3.92**	3.76	4.05	0.094	17	**3.67**	3.50	3.79	0.090	3.63	12	**3.78**	3.42	4.27	0.236
M^1M^3	7	**3.20**	3.00	3.45	0.146	12	**3.14**	3.05	3.21	0.054	17	**3.02**	2.84	3.58	0.157	2.97	12	**3.09**	2.74	3.42	0.195
M^1M^2	7	**2.48**	2.32	2.65	0.107	12	**2.43**	2.32	2.49	0.058	17	**2.32**	2.20	2.43	0.068	2.31	12	**2.37**	2.15	2.68	0.136
CP^4	7	**2.54**	2.43	2.77	0.116	12	**2.44**	2.32	2.55	0.080	17	**2.35**	2.23	2.49	0.083	2.45	12	**2.54**	2.35	2.82	0.165
P^2P^3	7	**0.76**	0.68	0.82	0.049	12	**0.65**	0.51	0.74	0.057	17	**0.72**	0.59	0.77	0.055	0.72	12	**0.80**	0.71	0.92	0.067
LMd	6	**9.79**	9.52	10.45	0.342	12	**9.67**	9.46	9.96	0.169	14	**9.32**	8.93	9.63	0.202	9.31	12	**10.09**	9.76	10.42	0.219
ACo	6	**2.67**	2.53	2.89	0.149	12	**2.74**	2.57	2.97	0.114	16	**2.74**	2.61	2.94	0.085	2.61	11	**2.82**	2.58	2.98	0.128
IM_3	7	**6.65**	6.34	7.14	0.257	12	**6.50**	6.39	6.61	0.092	17	**6.25**	5.94	6.49	0.136	6.34	12	**6.79**	6.43	7.22	0.233
CM_3	7	**5.59**	5.34	5.97	0.218	12	**5.52**	5.35	5.82	0.126	17	**5.26**	5.01	5.48	0.126	5.24	13	**5.71**	5.47	6.11	0.188
P_4M_3	7	**4.20**	3.89	4.45	0.174	12	**4.20**	4.08	4.29	0.076	17	**3.99**	3.79	4.13	0.091	3.95	12	**4.09**	3.82	4.58	0.268
M_1M_3	7	**3.50**	3.18	3.63	0.163	12	**3.49**	3.37	3.61	0.071	17	**3.32**	3.13	3.42	0.087	3.53	12	**3.45**	3.16	3.79	0.194
CP_4	7	**2.28**	2.18	2.54	0.122	12	**2.15**	2.04	2.28	0.085	17	**2.12**	1.98	2.24	0.078	2.15	12	**2.33**	2.20	2.54	0.117
P_2P_3	7	**0.87**	0.81	0.98	0.066	12	**0.78**	0.71	0.85	0.038	17	**0.82**	0.74	0.90	0.051	0.82	12	**0.91**	0.85	0.98	0.044
LCn	7	**0.85**	0.80	0.90	0.044	12	**0.95**	0.90	1.01	0.031	17	**0.82**	0.73	0.91	0.040	0.82	12	**0.83**	0.74	0.95	0.053
LaCn	7	**0.67**	0.61	0.75	0.046	12	**0.69**	0.61	0.75	0.040	17	**0.63**	0.58	0.68	0.034	0.65	12	**0.68**	0.63	0.80	0.045
P^3	7	**0.35**	0.29	0.39	0.031	12	**0.31**	0.22	0.39	0.046	17	**0.36**	0.29	0.43	0.032	0.35	12	**0.37**	0.30	0.42	0.035
P_3	7	**0.39**	0.37	0.43	0.030	12	**0.34**	0.30	0.38	0.027	17	**0.38**	0.29	0.43	0.036	0.38	12	**0.42**	0.36	0.47	0.034
ACin	7	**0.13**	0.06	0.17	0.041	12	**0.10**	0.04	0.21	0.045	17	**0.14**	0.10	0.17	0.023	0.14	8	**0.26**	0.20	0.31	0.041
P^4	7	**1.25**	1.09	1.37	0.088	12	**1.28**	1.18	1.35	0.052	17	**1.07**	0.97	1.16	0.048	1.22	12	**1.23**	1.09	1.38	0.092
M^1	7	**1.47**	1.40	1.63	0.089	12	**1.42**	1.30	1.48	0.053	17	**1.36**	1.18	1.47	0.064	1.38	12	**1.44**	1.26	1.58	0.092
M^2	7	**1.61**	1.53	1.74	0.070	12	**1.59**	1.46	1.65	0.056	17	**1.56**	1.46	1.65	0.047	1.56	12	**1.58**	1.45	1.72	0.089
M^3	7	**1.54**	1.43	1.60	0.053	12	**1.47**	1.37	1.55	0.053	17	**1.41**	1.34	1.50	0.047	1.42	12	**1.43**	1.32	1.61	0.097

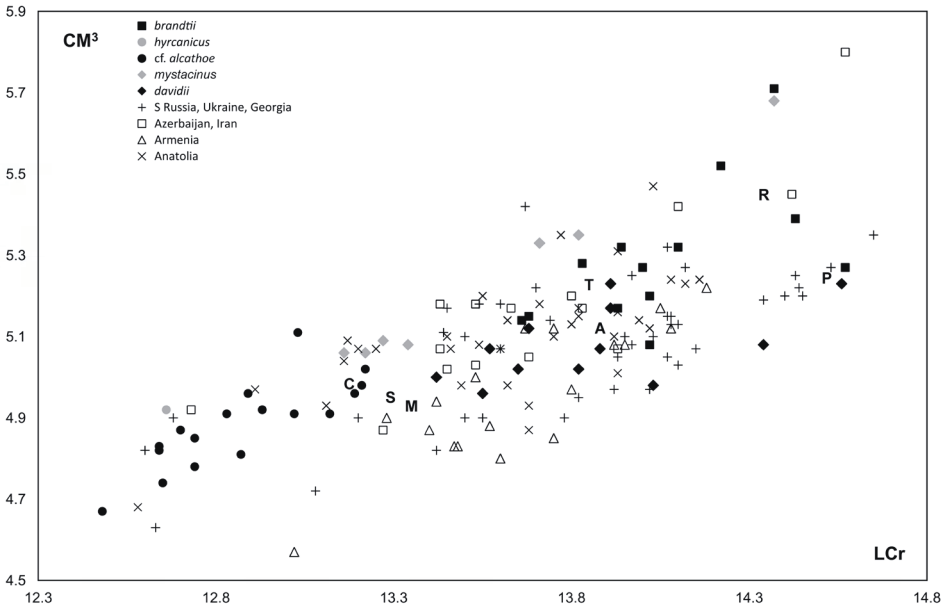

Figure 2. Bivariate plot of the examined samples of the *Myotis mystacinus* morphogroup from the Caucasus region: greatest length of skull (LCr) against the length of the upper tooth-row (CM^3). The closed symbols denote specimens identified with the help of genetic analysis (with the exception of *M. brandtii*, for details see text), open symbols all other specimens (arranged to geographical sets); bold capital letters denote holotype specimens of the following taxa: A – *Myotis mystacinus aurascens* Kuzâkin, 1935; C – *Myotis mystacinus caucasicus* Tsytsulina, 2000; M – *Myotis meinertzhageni* Thomas, 1926; P – *Myotis mystacinus popovi* Strelkov, 1983; R – *Myotis mystacinus pamirensis* Kuzâkin, 1935; S – *Myotis mystacinus sogdianus* Kuzâkin, 1934; T – *Myotis mystacinus transcaspicus* Ogneff & Heptner, 1928.

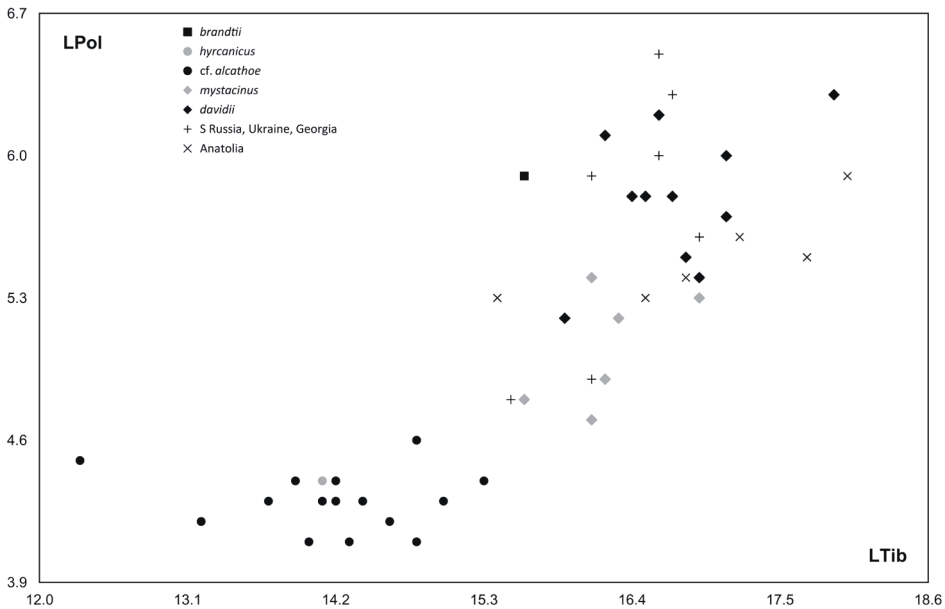

Figure 3. Bivariate plot of the examined samples of the *Myotis mystacinus* morphogroup from the Caucasus region: tibia length (LTib) against the thumb length (LPol). For explanations see Figure 2.

second upper premolars (P^3) positioned mostly in the axis of the tooth-row (mean P^3pos 1.65), third upper premolars (P^4) bearing a medium-sized cingular cusp (ACin 0.10–0.17 mm), and mesiodistally short upper canines (LCn/CM^3 0.15–0.18), their crowns being almost rounded (CnR 1.19–1.46).

Bats of lineage I, *M. mystacinus*, were medium-to large-sized (LAt 34.4–36.1 mm, LCr 13.1–14.4 mm),

with medium-sized thumbs (4.7–5.4 mm) and long tibiae (15.6–16.9 mm). Their skulls showed a relatively high (ANc/LCr 0.34–0.37, ANc/LaN 0.70–0.76) and broad (LaN/LCr 0.48–0.50) braincase, relatively low coronoid processes of the mandible (ACo/LMd 0.26–0.29), relatively narrow rostrum (CC/CM^3 0.61–0.65), and relatively medium-sized upper unicuspidal tooth-rows, C–P^4 (CP^4/M^1M^3 0.78–0.85). These bats possessed medium-sized molariform teeth (MR 1.5–2.5) and rather large premolars (P^2P^3 0.68–0.82 mm, P^3/LCn 0.36–0.46, P_3 0.37–0.43 mm, P^2P^3/LCr 0.051–0.062), relatively large third upper molars (M^3/M^1 0.96–1.12), second upper premolars (P^3) positioned mostly in the axis of the tooth-row (mean P^3pos 1.14), third upper premolars (P^4) bearing a very low to medium-sized cingular cusp (ACin 0.06–0.17 mm), and mesiodistally short upper canines (LCn/CM^3 0.16–0.18), their crowns being almost rounded (CnR 1.19–1.37). Two sublineages of this lineage (Ia and Ib, see Figure 1) represented two size-defined forms (which almost do not overlap in their dimensions), and the bats of the Greater Caucasus were smaller (LCr 13.1–13.8 mm) than the bats of Azerbaijan and North-Western Iran (LCr 14.4 mm); these two forms also slightly differed in some relative dimensions.

Bats of lineage II, *M. davidii*, were medium-sized to large (LAt 33.4–37.2 mm, LCr 13.4–14.6 mm), with long thumbs (5.2–6.3 mm) and tibiae (15.9–17.9 mm). Their skulls showed a relatively high (ANc/LCr 0.33–0.37, ANc/LaN 0.69–0.74) and broad (LaN/LCr 0.48–0.51) braincase, relatively medium-sized coronoid processes of the mandible (ACo/LMd 0.27–0.30), relatively wide rostrum (CC/CM^3 0.63–0.73), and relatively short upper unicuspidal tooth-rows, C–P^4 (CP^4/M^1M^3 0.73–0.80); in comparison with the bats of lineage I, these bats showed relatively short tooth-rows (CM^3/LCr 0.35–0.38, vs. 0.38–0.40). These bats possessed rather gracile molariform teeth (MR 0.5–2.5) and small premolars (P^2P^3 0.51–0.74 mm, P^3/LCn 0.24–0.40, P_3 0.30–0.38 mm, P^2P^3/LCr 0.037–0.054), relatively large third upper molars (M^3/M^1 0.97–1.08), second upper premolars (P^3) positioned in most cases medially from the axis of the tooth-row (mean P^3pos 1.92), third upper premolars (P^4) bearing a very low to medium-sized cingular cusp (ACin 0.04–0.21 mm), and mesiodistally long upper canines (LCn/CM^3 0.18–0.20), their crowns being rhomboid and pointed distally (CnR 1.29–1.51). This morphotype was represented by two size-defined geographical forms (broadly overlapping in their dimensions), which, however, were not reflected in the genetic subdivision. The bats from Crimea were on average large-sized (LCr 13.6–14.6 mm), while the bats from the Greater Caucasus and Iran were on average small-sized (LCr 13.4–14.3 mm).

3.3. Geographical distribution of particular morphotypes

The morphometric data obtained from 111 additional specimens of the *M. mystacinus* morphogroup coming from various parts of the Caucasus region that were not examined by molecular genetic methods enabled us to assign some of them to the above described morphotypes/lineages, based on statistical comparison (PCA) with the data from genetically identified bats. The clustering of particular specimens was tested by seven separate analyses: 1) analysis of all cranial dimensions and their indices, 2) analysis of all cranial dimensions, 3) analysis of cranial dimension indices, 4) analysis of all dental dimensions and their indices, 5) analysis of all dental dimensions, 6) analysis of dental dimension indices, and 7) analysis of canine and premolar dimensions and indices. Results of some of these analyses are presented in Figures 4–6. However, since the morphotypes overlapped in their particular dimension ranges to some extent, the assignation of the specimens to a certain morphotype was possible only in a part of the compared material. On the other hand, this comparison helped to describe the distribution range of the lineages/morphotypes in the respective region and also to affiliate the available type material of the group to the particular lineages; see Appendix 2.1. for data on all identified specimens.

M. brandtii, lineage VI, represented a very typical morphotype and although only two specimens from the respective region were examined with the help of the genetic analysis, altogether 13 bats of this morphotype were identified (Figures 4–6). These specimens originated from Crimea, from the Greater Caucasus of Russia (Krasnodar and Karachaevo-Cherkessia Provinces), from the Lesser Caucasus of Georgia (Bakuriani), and from the north-eastern (Rize Prov.) and central (Yozgat Prov.) parts of Anatolia.

The genetic analysis identified the morphotype representing lineages IV and V in two distant areas of the Caucasus region; 17 specimens (plus two biopsy samples) originated from the western part of the Greater Caucasus of Russia – solely from Krasnodar Province (*M.* cf. *alcathoe*) – and one specimen was collected in Northern Iran – Golestan Province (*M. hyrcanicus*). The combination of results of factor analyses of cranial and dental dimensions and their indices (Figures 4 and 5) clearly indicated six additional specimens to pertain to this morphotype: four specimens from the Greater Caucasus of Russia (Krasnodar and North Ossetia Provinces) and two specimens from the north-eastern part of Anatolia (Artvin and Erzurum Provinces). The morphological comparison did not identify whether these additional specimens belonged to lineage IV or to lineage V.

In *M. mystacinus* s.str., i.e. lineage I, seven specimens (plus five biopsy samples) were identified with the help of

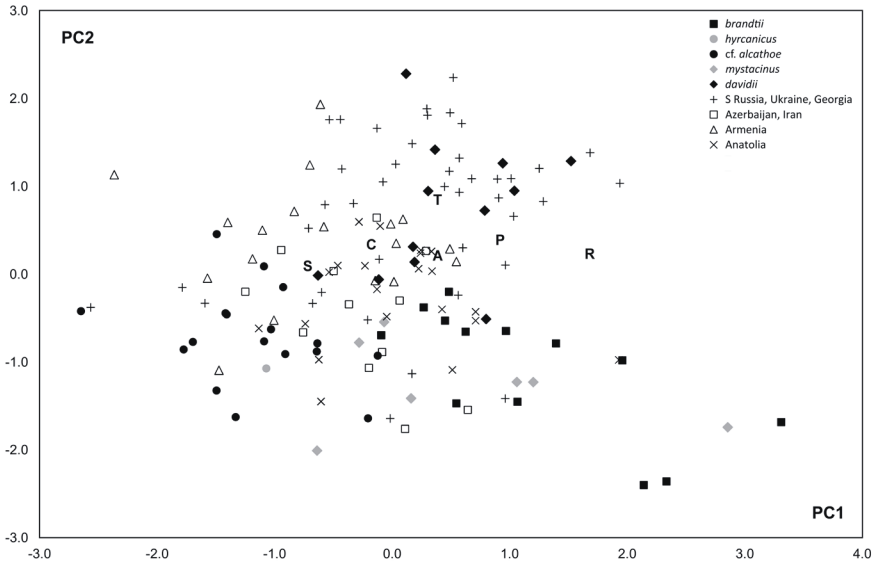

Figure 4. Bivariate plot of the examined samples of the *Myotis mystacinus* morphogroup from the Caucasus region: results of the principal component analysis of all skull dimensions and relative dimensions. For explanations see Figure 2.

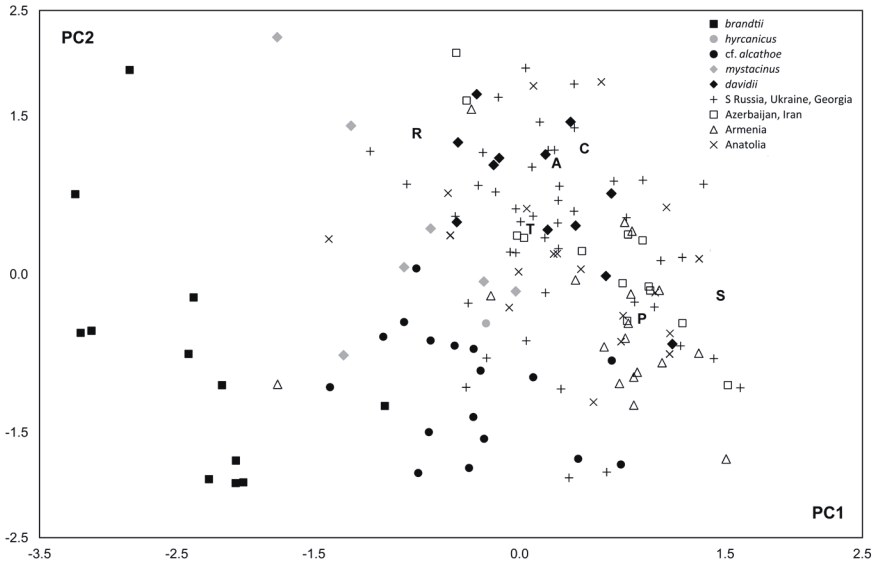

Figure 5. Bivariate plot of the examined samples of the *Myotis mystacinus* morphogroup from the Caucasus region: results of the principal component analysis of all tooth dimensions and relative dimensions. For explanations see Figure 2.

the genetic analysis. Nine individuals originated from the northern slopes of the Greater Caucasus of Russia, both from the western (Krasnodar and Adygea Provinces) and eastern (Dagestan Prov.) parts of this mountain range; two bats originated from the southern slopes of the Greater Caucasus in Azerbaijan and one specimen came from the north-western part of Iran (Ardabil Prov.). The combined results from factor analyses of cranial and dental dimensions indicated 13 additional specimens to belong to this lineage: five specimens from the Greater Caucasus range of Russia (Krasnodar and Stavropol' Provinces) and of Georgia (Abkhazia and Kakheti Provinces), two specimens from the south-eastern part of this range in Azerbaijan (Qəbələ and Xaçmaz Districts), two specimens from Eastern Anatolia (Iğdır and Van Provinces), and one specimen from the southern coast of Anatolia (Mersin Prov.). Three BMNH specimens collected in Qutur Su in the Ardabil Province of North-Western Iran (cf. Harrison, 1963) represented the same morphotype as the individual identified genetically (NMP 94105), originating also from

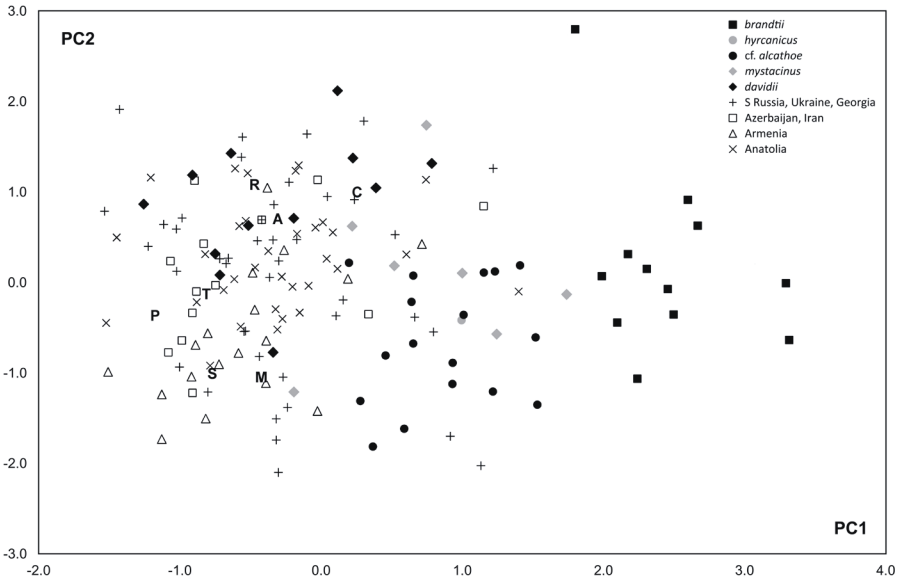

Figure 6. Bivariate plot of the examined samples of the *Myotis mystacinus* morphogroup from the Caucasus region: results of the principal component analysis of the dimensions and relative dimensions of upper canines and premolars. For explanations see Figure 2.

this site, and thus were also assigned to this lineage (see also Benda et al., 2012).

M. davidii, lineage II, comprised twelve specimens and eleven additional biopsy samples that were identified with the help of molecular genetic analysis. These samples originated from Crimea (four samples), the whole extent of the Greater Caucasus of Russia (16 samples from Krasnodar, Adygea, Stavropol', and Dagestan Provinces), Northern Azerbaijan (one sample), and North-Western Iran (two samples from Azarbaijan-e Gharbi Prov.). The combination of results from factor analyses of cranial and dental dimensions and their indices (Figures 4–6) selected 63 additional specimens of *M. davidii* (i.e. more than a half of all compared bats and more than two-thirds of the identified bats) in the morphologically examined material from the respective region. The areas of origin of most of these specimens conform to the areas of origin of the genetically identified bats, but additional specimens were identified also from the steppe region of Southern Ukraine and Russia, from Georgia, and from various parts of Azerbaijan and Anatolia. From Crimea, eleven additional specimens were identified, i.e. all the available bats from this peninsula (with the only exception of one *M. brandtii*, see above); seven identified specimens originated from the southern Ukrainian-Russian border regions (Kherson, Donetsk, Melitopol', and Rostov-on-Don Provinces); 14 specimens were identified among bats originating from the northern slopes of the Greater Caucasus in Russia (Krasnodar, Stavropol', North Ossetia, Chechnya, and Dagestan Provinces) and three specimens from the southern slopes of this mountain chain in North-Western Azerbaijan and North-Eastern Georgia; four identified specimens originated from the Lesser Caucasus of Western Azerbaijan, one specimen from the arid steppes of South-Eastern Azerbaijan, and two specimens from the mountain plateau of North-Western Iran (Ardabil Prov.). In Anatolia, the sites of the identified specimens were scattered over a large part of the country; 14 specimens were available from the eastern and north-eastern parts of Anatolia (Kars, Iğdır, Van, Bitlis, Erzurum, and Erzincan Provinces), four specimens from Central Anatolia (Konya and Niğde Provinces), and four specimens from Western Anatolia (Manisa Prov.).

3.4. Taxonomic comparison of particular morphotypes

The morphometric analysis also enabled us to compare skull and dental parameters of all available holotype specimens of the names within the *M. mystacinus* morphogroup of South-West Asian origin, namely *aurascens*, *caucasicus*, *meinertzhageni*, *pamirensis*, *popovi*, *sogdianus*, and *transcaspicus*. All seven analyses (see also Figures 2 and 4–6) showed all these type specimens to be clustered with the specimens identified as *M. davidii*/lineage II (both genetically and morphologically identified); certain exceptions were represented by the holotypes of *sogdianus* and *caucasicus*. The former type was not clearly identified by the analyses of skull dimensions (as it clustered with the intermediate specimens of the morphospatial zone of overlaps among several morphotypes; Figure 4), but was very clearly indicated as *M. davidii* by the analyses of dental dimensions (Figures 5 and 6). On the other hand, the type of *caucasicus* was clearly accompanied by *M. davidii* specimens in the analyses of skull dimensions, but

in dental dimension it clustered fully or almost with the intermediate specimens in the zone of overlaps among morphotypes. Despite the latter partial uncertainties, all holotype specimens showed larger morphometric affinities to the *M. davidii* morphotype than to any other above defined morphotype. The same is true also for all examined paratypes of *popovi* (6 specimens; see also Strelkov, 1983a), originating from Crimea and Donetsk and Krasnodar Provinces. The type series of *caucasicus* is composed of three specimens (see Benda and Tsytsulina, 2000); the holotype (ZIN 83623) – as mentioned above – was shown to possess the *M. davidii* morphotype and this is also true for one paratype specimen (ZIN 83771); however, another paratype (ZIN 83008) was identified as *M. mystacinus* (see Appendix 2.1).

A slightly different result was obtained from the comparison of the genetically identified specimens of the particular lineages with the specimen set of *M. hajastanicus* Argiropulo, 1939 (that included also two paratype specimens) from Armenia, as it was redescribed by Benda and Tsytsulina (2000). Unfortunately, no specimens of this taxon were available for genetic examination; however, the results of factor analyses of cranial dimensions and their indices positioned the specimens of *M. hajastanicus* close to, but not inside, the morphospace of the samples of *M. davidii* (see also Figures 2 and 4). On the other hand, the results of factor analyses of dental dimensions and their indices positioned the Armenian samples very close to the *M. davidii* specimens, creating one common morphospace in some of the resulting plots (see also Figures 5 and 6).

Besides *popovi*, *caucasicus*, and *hajastanicus*, in all other names only holotype specimens were originally designated as the type material; all of them were examined here (see above).

3.5. Morphological comparison of *M.* cf. *alcathoe*

The bats of lineage IV, named *M.* cf. *alcathoe* by Gazarân (2009), were shown by the genetic analysis to be the closest relatives of the European populations of *M. alcathoe* s.str. (lineage III); the uncorrected genetic distance between these two lineages was relatively small (see above). However, morphometric comparison of the available museum material belonging to these two lineages indicated almost identical morphotypes in both sets (Tables 2–4). The Caucasian specimens of *M.* cf. *alcathoe* were very similar to the specimens of *M. alcathoe* from Europe in the prevailing majority of metric parameters; the analysis of variance revealed only a few dimensions in which these two specimen sets showed statistically significant differences (Table 4). Most of the significant differences were found in the skull and rostrum widths ($P < 0.007$: CC, CC/LCr, CC/CM^3; $P < 0.05$: LaZ, LaI, LaN), in the relative height of the coronoid process ($P < 0.002$: ACo/LMd), in the tooth-row lengths ($P < 0.001$: M^1M^2; $P < 0.05$: P^4M^3, IM_3, P_4M_3, CP^4/M^1M^3), or in the thumb length ($P < 0.05$: LPol). No significant differences were found in the dental dimensions (except P^4 width and the upper molar metaloph massiveness) and their indices.

4. Discussion

The above presented results have revealed the existence of five genetic lineages of the *M. mystacinus* morphogroup in the broadly considered Caucasus region. Four of these lineages (I, II, IV, VI) were found to live in sympatry in the Caucasus Mountains and adjacent regions. The fifth lineage (V) represents the recently described species *M. hyrcanicus* from the forests of Northern Iran (Benda et al., 2012); this lineage can be undoubtedly considered as a species of its own, as it is sufficiently deeply separated from the closest relatives – the uncorrected genetic distances between *M. hyrcanicus* and other lineages of the morphogroup are larger than 9.5%, which sufficiently guarantees interspecific differences as suggested for mammals (Baker and Bradley, 2006). Because of the relative scarcity of museum material of bats from Iran, for the time being it is not possible to state which other lineages cooccur in these forests along with *M. hyrcanicus* (see the detailed reviews by DeBlase, 1980, and Benda et al., 2012). Considering the biogeographical zonation of the cis-Caspian region (see, e.g., Djamali et al., 2011), the distribution range of *M. hyrcanicus* could be expected to cover the whole belt of Hyrcanian forests between Golestan Province of Iran (incl.) and the Talysh Mts. of South-Eastern Azerbaijan. However, according to current knowledge, *M. hyrcanicus* cannot be considered as a member of the Caucasian fauna per se.

The bat specimens belonging to four lineages that were found to occur in sympatry in the Caucasus represented four distinct morphotypes. These lineages/morphotypes can be considered as four separate species, due to their sympatric occurrence in a wide area of the Caucasus as well as to sufficient genetic distances between them, exceeding 12.0% of the uncorrected genetic distance in the examined marker. Based on morphometric data, it was possible to identify these morphotypes in the prevailing majority (ca. 83%) of the examined museum specimens of bats from the region (the remaining specimens represented intermediate morphotypes that could not be assigned to a particular lineage).

The existence of several species of the *M. mystacinus* morphogroup in the Caucasus region was suggested already in several previous studies (Benda and Tsytsulina, 2000; Cyculina, 2000; Tsytsulina, 2000; Benda and Karataş, 2005; Gazarân, 2009). However, only the arrangement suggested by Gazarân (2009) is similar to that derived from the presented results; nevertheless, the latter study covered only the populations of the north-western part of the

Table 3. Relative dimensions and phenetic characters of the examined sample sets of the *Myotis mystacinus* morphogroup from the Caucasus region. See Section 2.3 for explanation of the dimension acronyms.

	Lineage I					Lineage II					Lineage IV					Lineage V	Lineage VI				
	M. mystacinus s.str.					*M. davidii*					*M.* cf. *alcathoe*					*M. hyrcanicus*	*M. brandtii*				
	n	**M**	min	max	SD	n	**M**	min	max	SD	n	**M**	min	max	SD		n	**M**	min	max	SD
CM^3/LCr	7	**0.386**	0.381	0.395	0.005	12	**0.367**	0.354	0.376	0.007	17	**0.379**	0.374	0.392	0.005	0.389	13	**0.377**	0.362	0.397	0.010
LaN/LCr	7	**0.487**	0.477	0.497	0.007	12	**0.491**	0.480	0.511	0.008	17	**0.485**	0.471	0.499	0.009	0.485	13	**0.490**	0.477	0.506	0.008
ANc/LCr	7	**0.354**	0.344	0.368	0.010	12	**0.352**	0.332	0.370	0.011	17	**0.357**	0.343	0.375	0.009	0.357	13	**0.337**	0.324	0.349	0.008
ANc/LaN	7	**0.727**	0.697	0.758	0.022	12	**0.716**	0.685	0.743	0.019	17	**0.735**	0.700	0.766	0.018	0.736	13	**0.687**	0.659	0.723	0.021
ACo/LMd	6	**0.273**	0.258	0.293	0.011	12	**0.283**	0.267	0.301	0.011	14	**0.296**	0.281	0.311	0.008	0.280	11	**0.279**	0.264	0.293	0.009
CC/LCr	6	**0.245**	0.237	0.252	0.006	12	**0.250**	0.234	0.259	0.008	17	**0.247**	0.239	0.258	0.005	0.258	13	**0.241**	0.229	0.252	0.007
CC/CM^3	6	**0.633**	0.613	0.647	0.013	12	**0.682**	0.625	0.725	0.028	17	**0.651**	0.624	0.676	0.016	0.665	13	**0.642**	0.618	0.671	0.018
CP^4/M^1M^3	7	**0.795**	0.775	0.846	0.025	12	**0.775**	0.729	0.804	0.023	17	**0.779**	0.666	0.845	0.044	0.823	12	**0.823**	0.758	0.894	0.040
P^2P^3/LCr	7	**0.056**	0.051	0.062	0.003	12	**0.047**	0.037	0.054	0.005	17	**0.056**	0.046	0.061	0.004	0.057	12	**0.057**	0.052	0.064	0.004
CnR	7	**1.275**	1.188	1.365	0.068	12	**1.391**	1.290	1.508	0.078	17	**1.290**	1.186	1.464	0.078	1.258	12	**1.227**	1.179	1.302	0.048
LCn/CM^3	7	**0.163**	0.157	0.178	0.007	12	**0.188**	0.178	0.200	0.007	17	**0.167**	0.152	0.183	0.007	0.166	12	**0.156**	0.143	0.167	0.007
P^3/LCn	7	**0.411**	0.359	0.461	0.037	12	**0.328**	0.244	0.398	0.047	17	**0.436**	0.341	0.481	0.034	0.423	12	**0.447**	0.377	0.506	0.036
M^3/M^1	7	**1.047**	0.962	1.119	0.050	12	**1.037**	0.965	1.080	0.034	17	**1.039**	0.936	1.159	0.052	1.030	12	**0.996**	0.940	1.083	0.042
MR	7	**2.071**	1.5	2.5	0.535	11	**1.318**	0.5	2.5	0.603	15	**1.800**	0.5	3.0	0.727	1.500	11	**3.545**	2.0	4.0	0.611
$ACin/P^4$	7	**0.105**	0.052	0.154	0.038	12	**0.080**	0.031	0.165	0.036	17	**0.129**	0.092	0.162	0.021	0.111	8	**0.202**	0.152	0.256	0.035
P^3pos	7	**1.14**	1	2	0.378	12	**1.92**	1	5	1.165	17	**1.65**	1	3	0.862	1	12	**1.00**	1	1	0.000
pcl	7	**0.43**	0.0	1.0	0.345	11	**0.18**	0.0	1.0	0.337	15	**0.33**	0.0	1.0	0.362	0.0	10	**0.90**	0.0	1.0	0.316
plph	7	**0.50**	0.0	1.0	0.289	12	**0.17**	0.0	1.0	0.326	16	**0.59**	0.0	1.0	0.272	0.5	11	**0.95**	0.5	1.0	0.151
mcl	7	**0.57**	0.0	1.0	0.450	11	**0.50**	0.0	1.0	0.224	14	**0.50**	0.0	1.0	0.340	0.5	12	**0.83**	0.5	1.0	0.246
mlph	7	**0.57**	0.5	1.0	0.189	12	**0.42**	0.0	1.0	0.359	16	**0.38**	0.0	1.0	0.342	0.5	12	**0.96**	0.5	1.0	0.144

Table 4. Results of the analysis of variance between the Caucasian and European sample sets of *Myotis alcathoe* and dimensions of the European samples of *M. alcathoe*. See Section 2.3 for explanation of the dimension acronyms. a – external, skull, and tooth dimensions (in millimetres); b – relative dimensions and phenetic characters.

a	ANOVA			Lineage III					**b**	ANOVA			Lineage III				
	results			*M. alcathoe* Europe						results			*M. alcathoe* Europe				
	df	F	p	n	**M**	min	max	SD		df	F	p	n	**M**	min	max	SD
LAt	40	0.025	0.876	25	**32.28**	27.2	35.3	1.401	CM^3/LCr	42	0.060	0.808	27	**0.379**	0.364	0.387	0.006
LPol	36	4.845	0.034	21	**4.39**	4.2	4.6	0.128	LaN/LCr	41	1.868	0.179	26	**0.490**	0.466	0.511	0.011
LTib	35	0.127	0.724	20	**14.25**	12.8	15.3	0.573	ANc/LCr	40	0.146	0.704	25	**0.356**	0.338	0.374	0.009
LCr	42	2.066	0.158	27	**12.99**	12.38	13.38	0.259	ANc/LaN	41	1.801	0.187	26	**0.727**	0.681	0.779	0.020
LCb	42	2.623	0.113	27	**12.43**	11.88	12.84	0.241	ACo/LMd	40	12.539	0.001	28	**0.289**	0.273	0.302	0.006
LaZ	31	5.661	0.024	19	**8.09**	7.57	8.43	0.202	CC/LCr	41	9.547	0.004	26	**0.254**	0.237	0.266	0.008
LaI	43	6.301	0.016	28	**3.25**	3.07	3.48	0.098	CC/CM^3	42	8.464	0.006	27	**0.668**	0.621	0.704	0.022
LaInf	43	0.377	0.543	28	**3.23**	3.03	3.41	0.092	CP^4/M^1M^3	43	4.704	0.036	28	**0.806**	0.688	0.877	0.037
LaN	42	5.498	0.024	27	**6.35**	6.01	6.64	0.145	P^2P^3/LCr	42	0.356	0.554	27	**0.056**	0.050	0.064	0.004
AN	42	0.816	0.371	27	**4.62**	4.39	4.75	0.111	CnR	43	0.687	0.412	28	**1.306**	1.200	1.397	0.053
CC	42	13.766	0.001	27	**3.29**	3.02	3.43	0.103	LCn/CM^3	43	0.122	0.728	28	**0.168**	0.154	0.182	0.008
M^3M^3	42	0.651	0.424	28	**5.16**	4.75	5.36	0.111	P^3/LCn	43	1.856	0.180	28	**0.422**	0.342	0.494	0.031
IM^3	42	3.157	0.083	27	**5.97**	5.70	6.16	0.115	M^3/M^1	43	0.003	0.957	28	**1.038**	0.984	1.116	0.032
CM^3	43	0.806	0.374	28	**4.91**	4.68	5.09	0.101	MR	41	0.004	0.951	28	**1.786**	0.5	3.0	0.726
P^4M^3	43	6.953	0.012	28	**3.59**	3.34	3.76	0.101	$ACin/P^4$	43	1.630	0.209	28	**0.137**	0.093	0.168	0.021
M^1M^3	43	3.434	0.071	28	**2.95**	2.76	3.42	0.125	P^3pos	42	0.922	0.342	27	**1.43**	1	3	0.661
M^1M^2	43	16.282	0.000	28	**2.24**	2.09	2.34	0.061	pcl	41	3.817	0.058	28	**0.54**	0.0	1.0	0.302
CP^4	43	0.415	0.523	28	**2.37**	2.17	2.59	0.108	plph	42	0.143	0.707	28	**0.63**	0.0	1.0	0.259
P^2P^3	43	0.921	0.343	28	**0.73**	0.66	0.82	0.047	mcl	40	0.096	0.758	28	**0.46**	0.0	1.0	0.358
LMd	40	0.523	0.474	28	**9.37**	8.92	9.70	0.198	mlph	42	5.199	0.028	28	**0.16**	0.0	1.0	0.274
ACo	42	2.035	0.161	28	**2.71**	2.53	2.86	0.085									
IM_3	43	4.228	0.046	28	**6.32**	6.04	6.52	0.108									
CM_3	43	1.767	0.191	28	**5.31**	5.01	5.49	0.108									
P_4M_3	43	7.067	0.011	28	**3.91**	3.58	4.03	0.107									
M_1M_3	43	2.995	0.091	28	**3.27**	3.00	3.37	0.089									
CP_4	43	0.006	0.941	28	**2.12**	1.94	2.24	0.093									
P_2P_3	43	1.083	0.304	28	**0.84**	0.75	0.90	0.041									
LCn	43	0.527	0.472	28	**0.83**	0.75	0.89	0.036									
LaCn	43	0.036	0.851	28	**0.63**	0.54	0.69	0.033									
P^3	43	0.698	0.408	28	**0.35**	0.27	0.41	0.027									
P_3	43	3.833	0.057	28	**0.36**	0.28	0.41	0.030									
ACin	43	3.708	0.061	28	**0.15**	0.10	0.19	0.023									
P^4	43	5.555	0.023	28	**1.11**	1.02	1.21	0.047									
M^1	43	0.164	0.687	28	**1.35**	1.27	1.42	0.044									
M^2	43	2.114	0.153	28	**1.54**	1.40	1.63	0.056									
M^3	43	0.153	0.697	28	**1.41**	1.29	1.51	0.048									

Greater Caucasus. All the studies prior to Gazarân (2009) assessed solely the morphological and morphometric data on skulls and teeth, and they did not reveal morphotype/lineage IV, here named *M.* cf. *alcathoe*; on the other hand, these studies suggested more distinct forms to be present within the single morphotype/lineage II, namely *M. nipalensis* and *M. aurascens* (differentiated mainly by their body size). The present results as well as the broad-scale molecular genetic analysis by Tsytsulina et al. (2012) clearly show all populations referred to the latter two names as belonging to a single evolutionary lineage. Since Tsytsulina et al. (2012) demonstrated a broad distribution of this lineage, Benda et al. (2012), based on morphological comparison of the type material, suggested to use the species name *M. davidii* for this lineage/species, a name originating from North-Eastern China (Peters, 1869). Thus, the taxonomic and biogeographical arrangements of the *M. mystacinus* morphogroup as suggested for the Caucasus region by Benda and Tsytsulina (2000) and consequent authors (namely Benda and Karataş, 2005) have to be revised in large part. The review of particular species (lineages/morphotypes) is given below.

M. davidii – i.e. lineage II – was shown to be the most widespread and also most abundant form of the morphogroup in the Caucasus region and adjacent areas; the identified specimens originated from all parts of the respective area, including southern parts of Ukraine and Russia (incl. Crimea), the Greater Caucasus of Russia and Georgia, all altitudinal zones of Azerbaijan, mountains of North-Western Iran, and the whole area of the Anatolian plateau. Concerning the geographical range as well as the occupied habitats (arid lowland steppes to mountain ecologica plasticityl and forests), *M. davidii* showed the largest plasticity within its distribution in the Caucasus region, although a certain preference for open habitats seems to prevail. However, as Tsytsulina et al. (2012) demonstrated, this species as a whole has a broad range stretching from Eastern Europe to Korea (including the East European steppes, West Turkestan deserts, and Mongolian arid plateau), and it creates a large number of ecomorphotypes, differing in body size and colouration (Strelkov, 1983a; Benda and Tsytsulina, 2000). From this extremely huge range a high number of forms were described (Dobson, 1871; Bobrinskoj, 1926, 1929; Thomas, 1926; Ogneff and Heptner, 1928; Kuzâkin, 1934, 1935; Strelkov, 1983a; Kruskop and Borissenko, 1996; Benda and Tsytsulina, 2000); according to the morphological comparison of the type material, the names *meinertzhageni* Thomas, 1926, *transcaspicus* Ogneff & Heptner, 1928, *sogdianus* Kuzâkin, 1934, *aurascens* Kuzâkin, 1935, *pamirensis* Kuzâkin, 1935, *popovi* Strelkov, 1983, and *caucasicus* Tsytsulina, 2000 represent junior synonyms of *M. davidii*. Based on morphology, genetic traits, and biogeographical grounds (Kruskop et al., 2012; Tsytsulina et al., 2012), the names *nipalensis* Dobson, 1871 and *mongolicus* Kruskop & Borissenko, 1996 also belong to this lineage. On the other hand, the East Turkestan/Tibetan populations described under the names *przewalskii* Bobrinskoj, 1926 and *kukunorensis* Bobrinskoj, 1929, as well as the Balkan populations recently named *bulgaricus* Heinrich, 1936 (see, e.g., Mayer et al., 2007; Volleth and Heller, 2012), which were considered as synonyms of either *aurascens* or *nipalensis* by Benda and Tsytsulina (2000) and Benda and Karataş (2005), require a new, very thorough multidisciplinary evaluation as they perhaps represent a more complex topic (see Mayer and von Helversen, 2001; Mayer et al., 2007; Tsytsulina et al., 2012; etc.). However, the taxonomic situation of the *M. davidii* lineage/morphotype in South-West Asia now seems to be more simple; it comprises one species, possessing a typical tooth pattern (see Section 3.2), but being extremely variable in metric traits and in general ecological requirements.

M. mystacinus s.str. – lineage I – was found to be rarer in the examined material of specimens from the Caucasus than the previous species; however, the distribution range is similarly wide within the region. Most of the identified specimens come from the Greater Caucasus of Russia, Georgia, and Azerbaijan, but some specimens were found also in North-Western Iran and in Eastern and Southern Anatolia. This species seems to prefer rather forested mountain habitats, although not all records are available from the forest zone of the Middle East/Caucasus. *M. mystacinus* is represented by two rather deeply separated (3.6%–4.2%) sublineages in the region, one in the Russian part of the Greater Caucasus, representing a part of the European populations (comprising also specimens from Central Europe and the Balkans), and the other in Azerbaijan and Iran. These two sublineages create two morphological forms differing considerably in body size: the Russian Caucasian bats are smaller (similar in size to Central European samples of *M. mystacinus*; see, e.g., Benda and Tsytsulina, 2000), while the Azerbaijani-Iranian ones are larger (for details, see Section 3.2). However, for the time being, it is not possible to solve this dichotomy simply by means of classical taxonomy and consider the sublineages as two subspecies of *M. mystacinus*. The European sublineage comprises both specimens of the Central European small-sized morphotype (regarded traditionally as the nominotypical form) and of the Balkan large-sized form, regarded as *M. aurascens* by Benda and Tsytsulina (2000) and as *M. mystacinus bulgaricus* by Mayer et al. (2007), Volleth and Heller (2012), and Dietz and Kiefer (2014). Since two clearly distinct morphological forms exist within one sublineage, the taxonomic evaluation of the mutual positions of two sublineages of *M. mystacinus* detected in the Caucasus region and their

relationships to other populations of the species requires a very profound broad-scale analysis of various markers. On the other hand, this complexity partially explains the confusing interpretation of interpopulation relationships suggested by Benda and Tsytsulina (2000), who assigned the South Caucasian large-sized populations of *M. mystacinus* to a separate species (*M. aurascens*) and the North Caucasian small-sized bats, which were similar to the Central European samples, to *M. mystacinus* (for more details see also discussion of this topic by Benda et al., 2012). The results of the present molecular genetic analysis did not support the delimitation of the North Caucasian populations of *M. mystacinus* into a separate subspecies, *M. m. caucasicus* (suggested by Benda and Tsytsulina, 2000), as they belong to the same sublineage as the nominotypical form, and, further, the morphometric analysis showed the name *caucasicus* to be regarded as a synonym of *M. davidii* and thus unavailable for designation of any form within the *M. mystacinus* rank (one paratype of *caucasicus* was identified as *M. mystacinus*; however, the paratype is not a name-bearing type specimen).

M. brandtii – lineage VI – was identified in specimens originating only from the western part of the broader Caucasus region, i.e. from Crimea, the western part of the Greater Caucasus of Russia, the Lesser Caucasus of Georgia, and from the north-eastern and central parts of Anatolia. This geographical pattern, covering mainly the elevated forested areas of the region, conforms to that reported by a series of previous authors (Strelkov, 1983b; Albayrak, 1991, 2003; Benda and Karataş, 2005; Gazarân et al., 2011). *M. brandtii* is a Eurasian species that belongs to the New World evolutionary clade of the genus *Myotis* as the only species along with *M. sibiricus* (Kaŝenko, 1905), i.e. it is phylogenetically unrelated to other species of the *M. mystacinus* morphogroup (Ruedi and Mayer, 2001; Stadelmann et al., 2004; Kruskop et al., 2012; Ruedi et al., 2013). The phylogenetic separation of *M. brandtii* conforms to the physical exclusivity of this bat; it represents the most peculiar morphotype within the morphogroup with characteristically built skull, teeth, and penis (see Section 3.2 and the review by Benda and Tsytsulina, 2000). Thus, its identification solely on morphological grounds is possible and fully reliable in most cases. The results of the molecular genetic analysis indicated *M. brandtii* as a relatively uniform species; only one haplotype of the cyt *b* gene was obtained from specimens originating from extremely distant parts of the European species range: from the Baltic area, Western Balkans, Crimea, and the Caucasus. This suggests a relatively recent spreading of this species over the extensive areas of the West Palaearctic forest zone.

The last species of the morphogroup inhabiting the Caucasus region, here named lineage IV or *M.* cf. *alcathoe* in accordance with Gazarân (2009), was confirmed only from Krasnodar Province of the Russian Caucasus. However, bats of the respective morphotype were found in one additional province of the northern part of the Greater Caucasus of Russia and in North-Eastern Anatolia, i.e. in forested mountain areas. This range resembles that of *M. brandtii* in the respective region and it is possible that *M.* cf. *alcathoe* represents a similar faunal element in the Caucasus; it implies that other Caucasian samples and the Anatolian bats could belong to lineage IV rather than to lineage V (i.e. to *M. hyrcanicus*, identified only from the easternmost part of the Hyrcanian forest zone in Iran, see above), both representing similar morphotypes. All three species, *M. brandtii*, *M. hyrcanicus*, and *M.* cf. *alcathoe*, seem to represent similar ecological elements, associated with deciduous or mixed forests of the region.

The comparison of morphometric parameters of *M.* cf. *alcathoe* from the Russian Caucasus with the European samples of *M. alcathoe* s.str. did not reveal any substantial difference between them; the Caucasian specimens showed only a slightly narrower skull, larger tooth-row dimensions, and a shorter thumb (for details see Section 3.5). Thus, almost identical morphotypes are present in both populations and it suggests that the Caucasus region is inhabited by a population identical or vicariant (and morphologically almost identical) to the recently described European bat, *M. alcathoe*. However, the results of the molecular genetic analysis showed samples of these two populations to be relatively distant, the uncorrected genetic distance being 4.6%–5.2% in the examined marker. Although this distance can suggest specific separation of these populations, their morphological uniformity and their allopatric distribution rather indicate a subspecific position of both taxa. A deeper separation of subspecies within clade B of the morphogroup than what is common in mammals (cf. Baker and Bradley, 2006) is also supported by a relatively deep separation of two mitochondrial sublineages within the European populations of *M. alcathoe*. It reached 2.9% in the examined marker; however, it may not affect the taxonomic positions of the sublineages, which exist in sympatry throughout Europe (see, e.g., Lučan et al., 2009; Jan et al., 2010) and represent one common taxon possessing two mitochondrial variants. Thus, we regard the bat populations of the Caucasus originally referred to *M.* cf. *alcathoe* by Gazarân (2009) as a part of the species rank of *M. alcathoe*, which, however, represents a separate subspecies. Since no name is available from the respective region to be assigned to this taxon (see above), it is described below as a new subspecies.

Because of the lack of genetic samples, we cannot fully evaluate the status of *M. hajastanicus*, a species suggested by Benda and Tsytsulina (2000) and Cyculina (2000) to

be endemic to the Sevan Lake Basin in Armenia (this conclusion was accepted, e.g., by Âvruân et al., 2002 and Simmons, 2005). The statistical comparison of the metric characters of these bats showed them to be most similar to *M. davidii* (lineage II) in dental traits, but somewhat separated in skull traits. It suggests close phylogenetic positions of *hajastanicus* and *davidii* morphotypes, and *M. hajastanicus* thus can be considered a form derived from lineage II. However, until genetic material of the respective population is available for molecular genetic comparison, the final solution of the taxonomic position of *M. hajastanicus* will remain open.

In conclusion, the combined results of analyses of two different types of evidence demonstrated an occurrence of five different species of the *Myotis mystacinus* morphogroup in the broader Caucasus region. *M. hyrcanicus* occurs in the Hyrcanian forest zone of Northern Iran, in allopatry to all other species. The other four species live in sympatry in the Caucasus Mountains and adjacent areas; *M. mystacinus* and *M. davidii* are broadly distributed throughout the region from the whole Northern Caucasus to Anatolia and North-Western Iran (*M. davidii* also in Crimea and adjacent steppes), and *M. brandtii* and *M. alcathoe* occur in limited ranges in the western part of the region, comprising the western part of the Greater Caucasus and North-Eastern Anatolia (*M. brandtii* also in Crimea, Georgia, and Central Anatolia). *M. davidii* seems to be the most widespread, morphologically plastic, and ecologically universal of the five species of the morphogroup, while *M. alcathoe* and *M. hyrcanicus* are geographically the most limited. While the intraspecific positions of the Caucasian populations of *M. mystacinus* and *M. davidii* remain unresolved (due to the unresolved intraspecific situations of these species as a whole), the populations of *M. brandtii* belong to the nominotypical form of this species, and the populations of *M. alcathoe* represent a newly described endemic subspecies, which is phylogenetically in a sister position to the nominotypical form of Europe; *M. hyrcanicus* is regarded a monotypic species. The taxonomic position of *M. hajastanicus* from Armenia has not yet been evaluated in full and the phylogenetic relationships of this taxon remain open.

4.1. Taxonomic description

Myotis alcathoe circassicus subsp. nov.

Holotype. Adult male (NMP 95309 [S+A]), Bol'šaâ Fanagorijskaâ Cave, Fanagorijskoe, Krasnodar Prov., Russia, 3 October 2007, leg. S. Gazarân.

Paratypes (9). 4 ♂♂ (NMP 95325–95328 [S+A]), Bol'šaâ Fanagorijskaâ Cave, Fanagorijskoe, Krasnodar Prov., Russia, 30 September 2008, leg. S. Gazarân; – 5 ♀♀ (NMP 95313–95317 [S+A]), Gebeus Mt., Gešebs, Krasnodar Prov., Russia, 11 July 2007, leg. S. Gazarân.

Type locality. Russia, Krasnodar Province [Краснодарский край], Bol'šaâ Fanagorijskaâ Cave [Большая Фанагорийская пещера], 11 km WSW of Fanagorijskoe [Фанагорийское]; 44°28′09″N, 38°58′40″E, ca. 340 m a.s.l.

Description. *Myotis alcathoe circassicus* subsp. nov. is a small representative of the genus as well as of the *Myotis mystacinus* morphogroup as defined by Benda and Karataş (2005), in most respects similar to the European *M. a. alcathoe* von Helversen & Heller, 2001 and Iranian *M. hyrcanicus* Benda, Reiter & Vallo, 2012. The size of the body and skull is small, forearm length 30.1–34.2 mm, ear length 13.0–14.6 mm, tragus length 5.3–6.0 mm, greatest length of skull 12.5–13.2 mm, and length of upper tooth-row (CM^3) 4.7–5.1 mm.

Skull is narrow, both in neurocranial and rostral parts (LaZ 7.6–8.2 mm, LaI 2.9–3.4 mm, LaN 5.9–6.5 mm, CC 3.0–3.3 mm), relatively narrower than in *M. a. alcathoe*, but similar to *M. hyrcanicus* (CC/LCr 0.24–0.26, CC/CM^3 0.62–0.68). Rostrum is relatively short, similarly as in *M. a. alcathoe* (Tables 3 and 4).

Teeth are large and massive; unicuspidal teeth are massive, upper canine is wide (in the labiopalatal aspect), its crown is rather rounded in occlusal view (CnR 1.19–1.46), second upper premolar is small (P^3 0.35 mm) in the tooth-row between P^2 and P^4 (i.e. not shifted palatally), the largest (third) upper premolar is rather small (P^4 0.97–1.16 mm), on average smaller than in *M. a. alcathoe*, bearing rather high cusp on the mesiopalatal margin of cingulum (ACin 0.10–0.17 mm); crowns of the upper molars are mesiodistally long, on average much longer than in *M. a. alcathoe* (M^1M^2 2.2–2.4 mm); upper molars are rather large, bearing moderately developed paralophi, metaconuli, and metalophi; the metalophi are on average more massive than in *M. a. alcathoe*.

Pelage colouration is brownish; bases of hairs are dark brown to blackish, distal parts of the dorsal hairs are brown, while those of the ventral hairs whitish or creamy, pale ochre on the neck. The face, ears, and wing membranes are pale greyish-brown, tips of the snout and ears are dark brown.

Genetics. In comparison with its closest relative, *M. a. alcathoe* von Helversen & Heller, 2001 from the western part of Europe, *M. a. circassicus* subsp. nov. shows a unique base position within the mitochondrial gene for cytochrome *b* (1140 bp) at 39 sites (i.e. 3.42% of the gene): 390 (A [in *M. a. alcathoe*] →C [in *M. a. circassicus* subsp. n.]), 90, 159, 237, 258, 777, 813, 882 (A→G), 528 (A→T), 304, 507 (C→A), 195, 724, 801, 993, 1014, 1068 (C→T), 562, 873, 945, 1134 (G→A), 81, 252 (T→A), 136, 145, 156, 174, 198, 561, 573, 684, 708, 784, 822, 879, 916, 975, 1056, and 1083 (T→C).

In comparison with the second closest relative, sister species *M. hyrcanicus* Benda, Reiter & Vallo, 2012 from Northern Iran, *M. a. circassicus* subsp. nov. shows a unique

base position within the respective mitochondrial gene at 109 sites (i.e. 9.56% of the gene): 90, 93, 159, 237, 258, 297, 369, 476, 516, 576, 777, 882, 936, 985, 1020, 1095 (A [in *M. hyrcanicus*] →G [in *M. a. circassicus* subsp. n.]), 528 (A→T), 304, 507, 737, 990 (C→A), 27, 69, 234, 249, 279, 358, 441, 513, 522, 555, 591, 618, 654, 672, 693, 714, 724, 741, 792, 841, 862, 885, 894, 909, 924, 958, 969, 986, 993, 1003, 1014, 1068, 1080, 1110, 1122 (C→T), 47, 102, 232, 348, 411, 466, 579, 582, 624, 855, 867, 876, 1032, 1056, 1098 (G→A), 390 (G→C), 525 (T→A), 24, 39, 60, 156, 165, 182, 186, 243, 273, 417, 420, 426, 450, 498, 573, 708, 710, 730, 736, 744, 804, 819, 874, 888, 891, 919, 948, 957, 970, 975, 1002, 1047, 1050, 1083, 1092, and 1125(T→C).

The complete sequences of the mitochondrial gene for cytochrome *b* of the type specimens are available in GenBank under accession numbers KU060278 (holotype sequence), KU060279, and KU060280 (paratypes).

Dimensions of the holotype. Forearm length 32.8 mm, thumb length 4.1 mm, tibia length 14.8 mm, greatest skull length 13.22 mm, condylobasal length 12.62 mm, zygomatic width 8.23 mm, interorbital width 3.32 mm, infraorbital width 3.24 mm, neurocranium width 6.47 mm, neurocranium height 4.53 mm, rostral width across upper canines (incl.) 3.33 mm, rostral width across third upper molars (incl.) 5.34 mm, length of upper tooth-row between first incisor and third molar (incl.) 6.09 mm, length of upper tooth-row between canine and third molar (incl.) 5.02 mm, length of upper tooth-row between third premolar and third molar (incl.) 3.79 mm, length of upper tooth-row between first and third molars (incl.) 3.03 mm, length of upper tooth-row between first and second molars (incl.) 2.34 mm, length of upper tooth-row between canine and third premolar (incl.) 2.45 mm, length of upper tooth-row between first and second premolars (incl.) 0.78 mm, mandible length 9.63 mm, coronoid height of mandible 2.94 mm, length of lower tooth-row between first incisor and third molar (incl.) 6.47 mm, length of lower tooth-row between canine and third molar (incl.) 5.48 mm, length of lower tooth-row between third premolar and third molar (incl.) 4.13 mm, length of lower tooth-row between first and third molars (incl.) 3.42 mm, length of lower tooth-row between canine and third premolar (incl.) 2.25 mm, length of lower tooth-row between first and second premolars (incl.) 0.87 mm, mesiodistal crown length of upper canine 0.83 mm, palatolabial crown width of upper canine 0.68 mm, mesiodistal crown length of second upper premolar 0.40 mm, mesiodistal crown length of second lower premolar 0.40 mm, height of cingular cusp on third upper premolar 0.16 mm, palatolabial crown width of fourth upper premolar 1.16 mm, palatolabial crown width of first upper molar 1.41 mm, palatolabial crown width of second upper molar 1.65 mm, palatolabial crown width of third upper molar 1.50 mm.

Etymology. The name *circassicus* reflects the origin of the type series as well as the area of distribution of the new subspecies (see Distribution). Circassia was a historical region (16th–19th centuries) in the forest zone of the North-Western Caucasus, roughly comprising the present territories of Krasnodar, Adygea and Karachaevo-Cherkessia Provinces of Russia. The above name of this region is a Latinised version of the name Cherkessia, used in Turkic languages for the Country of Adygeans (Cherkesses).

Distribution. *Myotis alcathoe circassicus* subsp. nov. is distributed in the forests of the northern slopes of the Greater Caucasus in Russia. Confirmed records are available from six sites of the westernmost part of this mountain range (see Appendix 1), most continuously covered by deciduous forests (Krasnodar Province). Considering the results of morphometric comparisons, *M. a. circassicus* subsp. nov. most probably has a broader distribution, covering also North Ossetia Province of Russia and Artvin and Erzurum Provinces of Turkey.

Nomenclatural acts. This work and the nomenclatural acts it contains have been registered in ZooBank. The ZooBank Life Science Identifier (LSID) for this publication is: http://zoobank.org/urn:lsid:zoobank.org:pub:89678140-FD70-4EA6-AA5F-02C21398D33B

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Appendix 1. List of specimens examined in the molecular genetic analysis; GBAN – GenBank accession number.

Haplotype	GBAN	Lineage	Country	Site	Coordinates	Voucher
hap1	KU060252	*M. mystacinus*	Russia	Guzeripl', Adygea Prov.	44°00′N, 40°08′E	NMP 95305
			Russia	Gebeus Mt., Gešebs, Krasnodar Prov.	44°23′N, 38°36′E	NMP 95321
			Russia	Gebeus Mt., Gešebs, Krasnodar Prov.	44°23′N, 38°36′E	NMP 95322
			Russia	Gebeus Mt., Gešebs, Krasnodar Prov.	44°23′N, 38°36′E	NMP 95323
			Russia	Psezuapse River, 30 km, Krasnodar Prov.	43°56′N, 39°31′E	NMP 95332
			Russia	Psezuapse River, 30 km, Krasnodar Prov.	43°56′N, 39°31′E	Biopsy
			Russia	Kurdžips River, Kurdžipskaâ, Adygea Prov.	44°30′N, 40°05′E	Biopsy
			Russia	Bol'šaâ Fanagorijskaâ Cave, Fanagorijskoe, Krasnodar Prov.	44°28′N, 38°59′E	Biopsy
hap2	KU060253	*M. mystacinus*	Russia	Berkubinskaâ Forest, Dagestan Prov.	41°41′N, 48°25′E	NMP 95311
hap3KU060255		*M. mystacinus*	Bulgaria	Gorna Breznica, Blagoevgrad Prov.	41°45′ N, 23°07′E	NMP 48342
			Greece	Sparta, Lakonia Dist., Peloponnese	37°05′N, 22°26′E	NMP 48346
hap4	KU060254	*M. mystacinus*	Czech Republic	Běstvina, Chrudim Dist.	49°50′N, 15°35′E	NMP 49492
			Czech Republic	Bolíkovice, Třebíč Dist.	49°08′N, 15°46′E	NMP 49497
			Montenegro	Vitoglav, Risan, Kotor Dist.	42°31′N, 18°41′E	NMP 90208
			Montenegro	Stabna, Plužine Dist.	43°10′N, 18°46′E	NMP 90226
hap5	KU060256	*M. mystacinus*	Greece	Simopoulo, Ilia Dist., Peloponnese	37°51′N, 21°32′E	NMP 49017
hap6	KU060257	*M. mystacinus*	Azerbaijan	Şəki, Şəki Dist.	41°12′N, 47°10′E	Biopsy
hap7	KU060258	*M. mystacinus*	Azerbaijan	Şəki, Şəki Dist.	41°12′N, 47°10′E	Biopsy
hap8	KU060259	*M. mystacinus*	Iran	Qutur Su, Ardabil Prov.	38°20′N, 47°51′E	NMP 94105
hap9	KU060262	*M. davidii*	Russia	Karamyk River, Sablinskoe, Stavropol' Prov.	44°30′N, 43°10′E	Biopsy

Appendix 1. (Continued).

hap10	KU060263	*M. davidii*	Russia	Egerskaâ Karaulka, Adygea Prov.	44°10′N, 39°50′E	NMP 95320
hap11	KU060260	*M. davidii*	Russia	Karamyk River, Sablinskoe, Stavropol’ Prov.	44°30′N, 43°10′E	Biopsy
			Russia	Karamyk River, Sablinskoe, Stavropol’ Prov.	44°30′N, 43°10′E	Biopsy
			Russia	Karamyk River, Sablinskoe, Stavropol’ Prov.	44°30′N, 43°10′E	Biopsy
			Russia	Karamyk River, Sablinskoe, Stavropol’ Prov.	44°30′N, 43°10′E	Biopsy
			Russia	Karamyk River, Sablinskoe, Stavropol’ Prov.	44°30′N, 43°10′E	Biopsy
			Russia	Karamyk River, Sablinskoe, Stavropol’ Prov.	44°30′N, 43°10′E	Biopsy
			Russia	Razvalka Mine, Voronov, Stavropol’ Prov.	44°10′N, 43°02′E	Biopsy
			Russia	Apšeronsk, Krasnodar Prov.	44°26′N, 39°44′E	NMP 95308
			Russia	Egerskaâ Karaulka, Adygea Prov.	44°10′N, 39°50′E	NMP 95318
			Russia	Egerskaâ Karaulka, Adygea Prov.	44°10′N, 39°50′E	NMP 95319
hap12	KU060261	*M. davidii*	Russia	Karamyk River, Sablinskoe, Stavropol’ Prov.	44°30′N, 43°10′E	Biopsy
			Russia	Karamyk River, Sablinskoe, Stavropol’ Prov.	44°30′N, 43°10′E	Biopsy
hap13	KU060265	*M. davidii*	Russia	Kumtor-Kala Station, Dagestan Prov.	43°00′N, 47°14′E	NMP 95303
			Russia	Kumtor-Kala Station, Dagestan Prov.	43°00′N, 47°14′E	NMP 95302
hap14	KU060264	*M. davidii*	Crimea	Suuk-Koba Cave, Čatyr-Dag Âjla, Simferopol’ Dist.	44°47′N, 34°17′E	NMP pb4354
			Crimea	Suuk-Koba Cave, Čatyr-Dag Âjla, Simferopol’ Dist.	44°47′N, 34°17′E	NMP pb4357
			Crimea	Kamenskoe, Lenino Dist.	45°17′N, 35°32′E	NMP pb4406
			Crimea	Kamenskoe, Lenino Dist.	45°17′N, 35°32′E	NMP pb4408
hap15	KU060266	*M. davidii*	Azerbaijan	Kiş, Şəki Dist.	41°15′N, 47°12′E	Biopsy
hap16	KU060267	*M. davidii*	Iran	Bastam, Azarbaijan-e Gharbi Prov.	38°53′N, 44°57′E	NMP 48119
			Iran	Bastam, Azarbaijan-e Gharbi Prov.	38°53′N, 44°57′E	NMP 48120

Appendix 1. (Continued).

hap17	KU060269	*M. alcathoe*	Czech Republic	Klíčava, Rakovník Dist.	50°04′N, 13°56′E	NMP 94580
hap18	KU060268	*M. alcathoe*	Czech Republic	Vůznice Reserve, Nižbor, Rakovník Dist.	50°02′N, 13°59′E	NMP 94582
			Czech Republic	Ledové sluje Cave, Čížov, Znojmo Dist.	48°53′N, 15°51′E	NMP 94577
			Czech Republic	Ledové sluje Cave, Čížov, Znojmo Dist.	48°53′N, 15°51′E	NMP 94575
			Czech Republic	Ledové sluje Cave, Čížov, Znojmo Dist.	48°53′N, 15°51′E	NMP 94571
			Czech Republic	Baštův Mill, Havraníky, Znojmo Dist.	48°49′N, 15°59′E	SMZ 6713
			Montenegro	Stabna, Plužine Dist.	43°10′N, 18°46′E	NMP 90228
			Czech Republic	Vůznice Reserve, Nižbor, Rakovník Dist.	50°02′N, 13°59′E	NMP 94569
			Czech Republic	Vůznice Reserve, Nižbor, Rakovník Dist.	50°02′N, 13°59′E	NMP 94570
			Czech Republic	Vlkov Pond, Šumná, Znojmo Dist.	48°56′N, 15°55′E	NMP 94584
hap19	KU060276	*M. alcathoe*	Bulgaria	Gorna Breznica, Blagoevgrad Prov.	41°45′N, 23°07′E	NMP 48343
hap20	KU060271	*M. alcathoe*	Slovakia	Stĺpová Cave, Šurice, Romavská Sobota Dist.	48°12′N, 19°55′E	NMP 50446
hap21	KU060272	*M. alcathoe*	Czech Republic	Ledové sluje Cave, Čížov, Znojmo Dist.	48°53′N, 15°51′E	NMP 94573
			Slovakia	Boťany, Trebišov Dist.	48°28′N, 22°07′E	NMP 94587
			Czech Republic	Ledové sluje Cave, Čížov, Znojmo Dist.	48°53′N, 15°51′E	NMP 94576
			Ukraine	Čizaj, Beregove, Zakarpats'ka Prov.	48°13′N, 22°38′E	Biopsy
hap22	KU060270	*M. alcathoe*	Czech Republic	Líšná, Přerov Dist.	49°24′N, 17°33′E	NMP 94578
			Czech Republic	Líšná, Přerov Dist.	49°24′N, 17°33′E	NMP 94579
			Czech Republic	Vůznice Reserve, Nižbor, Rakovník Dist.	50°02′N, 13°59′E	NMP 94581
			Czech Republic	Smrdutá Reserve, Chvalčov, Kroměříž Dist.	49°22′N, 17°45′E	NMP 94583
hap23	KU060273	*M. alcathoe*	Czech Republic	Tvořihráz, Znojmo Dist.	48°54′N, 16°07′E	NMP 94585
			Slovakia	Stĺpová Cave, Šurice, Romavská Sobota Dist.	48°12′N, 19°55′E	NMP 50447

Appendix 1. (Continued).

			Slovakia	Boťany, Trebišov Dist.	48°28′N, 22°07′E	NMP 94586
hap24	KU060277	*M. alcathoe*	Bulgaria	Gorna Breznica, Blagoevgrad Prov.	41°45′N, 23°07′E	NMP 48344
hap25	KU060274	*M. alcathoe*	Bulgaria	Malko Târnovo, Burgas Prov.	42°00′N, 27°31′E	Biopsy
hap26	KU060275	*M. alcathoe*	Bulgaria	Kaleto Cave, Mladežko, Burgas Prov.	42°09′N, 27°21′E	Biopsy
hap27	KU060280	*M.* cf. *alcathoe*	Russia	Utriš Peninsula, Krasnodar Prov.	44°47′N, 37°24′E	NMP 95306
hap28	KU060278	*M.* cf. *alcathoe*	Russia	Psekabs River, Thamaha, Krasnodar Prov.	44°39′N, 38°54′E	NMP 95307
			Russia	Bol'šaâ Fanagorijskaâ Cave, Fanagorijskoe, Krasnodar Prov.	44°28′N, 38°59′E	NMP 95309
			Russia	Gebeus Mt., Gešebs, Krasnodar Prov.	44°23′N, 38°36′E	NMP 95313
			Russia	Gebeus Mt., Gešebs, Krasnodar Prov.	44°23′N, 38°36′E	NMP 95314
			Russia	Gebeus Mt., Gešebs, Krasnodar Prov.	44°23′N, 38°36′E	NMP 95315
			Russia	Gebeus Mt., Gešebs, Krasnodar Prov.	44°23′N, 38°36′E	NMP 95316
			Russia	Gebeus Mt., Gešebs, Krasnodar Prov.	44°23′N, 38°36′E	NMP 95317
			Russia	Bol'šaâ Fanagorijskaâ Cave, Fanagorijskoe, Krasnodar Prov.	44°28′N, 38°59′E	NMP 95325
			Russia	Bol'šaâ Fanagorijskaâ Cave, Fanagorijskoe, Krasnodar Prov.	44°28′N, 38°59′E	NMP 95326
			Russia	Bol'šaâ Fanagorijskaâ Cave, Fanagorijskoe, Krasnodar Prov.	44°28′N, 38°59′E	NMP 95327
			Russia	Bol'šaâ Fanagorijskaâ Cave, Fanagorijskoe, Krasnodar Prov.	44°28′N, 38°59′E	NMP 95328
			Russia	Aše, Krasnodar Prov.	43°58′N, 39°16′E	NMP 95329
			Russia	Tahira Cave, Kalež, Krasnodar Prov.	44°01′N, 39°21′E	NMP 95331
			Russia	Utriš Peninsula, Krasnodar Prov.	44°47′N, 37°24′E	Biopsy
			Russia	Utriš Peninsula, Krasnodar Prov.	44°47′N, 37°24′E	Biopsy
hap29	KU060279	*M.* cf. *alcathoe*	Russia	Psekabs River, Thamaha, Krasnodar Prov.	44°39′N, 38°54′E	NMP 95312
			Russia	Bol'šaâ Fanagorijskaâ Cave, Fanagorijskoe, Krasnodar Prov.	44°28′N, 38°59′E	NMP 95324

Appendix 1. (Continued).

			Russia	Aše, Krasnodar Prov.	43°58′N, 39°16′E	NMP 95330
hap30	KU060281	*M. hyrcanicus*	Iran	Ali Abad, Golestan Prov.	36°53′N, 54°53′E	NMP 90857
hap31	KU060282	*M. brandtii*	Russia	Dzyhra Lake, Ahštyr', Krasnodar Prov.	43°32′N, 40°01′E	NMP 95310
			Russia	Staraâ Ladoga, Leningrad Prov.	60°01′N, 32°19′E	NMP 49272
			Crimea	Partizanskoe, Âlta Dist.	44°33′N, 34°15′E	NMP pb4345
			Montenegro	Stabna, Plužine Dist.	43°10′N, 18°46′E	NMP 90227
	JX570902	*Nyctalus noctula*				Heaney et al. (2012)
	JX570901	*Nyctalus leisleri*				Heaney et al. (2012)
	AF376834	*Vespertilio murinus*				Ruedi and Mayer (2001)

Appendix 2. List of specimens examined in the morphological comparison.

Appendix 2.1. List of identified specimens (*: identified with the help of genetic analysis, others by morphological comparison).

Myotis mystacinus (lineage I)
Azerbaijan (2): 1 ind. (NMP 48520 [S+B]), Kutakşen [= Qəbələ, Qəbələ Dist.], 7 August 1935, leg. N. Vereŝagin; – 1 ♂ (NMP 48540 [S+B]), Xaçmaz District, 24 June 1975, leg. I. K. Rahmatulina. – **Georgia** (2): 1 ♂ (NMP 95301 [S+A]), Kvanša Mt., Bzibskij Range (Abkhasia Prov.), 8 August 2003, leg. S. Gazarân; – 1 ♂ (ZIN 9286 [S+A]), Lagodehi [Kakheti Prov.], 25 July 1911, leg. K. Satunin. – **Iran** (4): 3 ♂♂ (BMNH 63.1196–1198 [S]), Gutur Su, N of Mt. Sabalan [Ardabil Prov.], 21 August 1961, leg. University of Wales Expedition; – 1 ♂* (NMP 94105 [S+A]), Qutur Su (Ardabil Prov.), 29 September 2011, leg. M. Andreas, P. Benda, A. Reiter and M. Uhrin. – **Russia** (9): 1 ♀ (ZIN 83008 [S+A], paratype of *Myotis mystacinus caucasicus* Tsytsulina, 2000), Adler (Krasnodar Prov.), 16 July 1997, leg. K. Cyculina; – 1 ♂* (NMP 95311 [S+A]), Berkubinskaâ Forest (Dagestan Prov.), 9 May 2008, leg. S. Gazarân; – 1 ♀ (NMP 95304 [S+A]), Èsto-Sadok, Krasnaâ Polâna (Krasnodar Prov.), 16 September 2008, leg. S. Gazarân; – 3 ♀♀* (NMP 95321–95323 [S+A]), Gebeus Mt., Gešebs (Krasnodar Prov.), 11 July 2007, leg. S. Gazarân; – 1 ♂* (NMP 95305 [S+A]), Guzeripl' (Adygea Prov.), June 2006, leg. S. Gazarân; – 1 ♀* (NMP 95332 [S+A]), Psezuapse River, 30 km (Krasnodar Prov.), 23 August 2007, leg. S. Gazarân; – 1 ♀ (ZIN 9178 [S+A]), Stavropol' [Stavropol' Prov.], date and collector unlisted. – **Turkey** (3): 1 ♂ (ZIN 9004 [S+A]), Aralyh (Erivan'skaâ Guberniâ) [= Aralık (Iğdır Prov.)], 1901, leg. K. Satunin; – 1 ♂ (ZMB 53250 [S]), Mersina, Kleinasien [= Mersin, İçel Prov.], date unlisted, leg. Siehe; – 1 ♂ (NMP 47915 [S+A]), Van Castle (Van Prov.), 28 July 1992, leg. P. Benda.

Myotis a. alcathoe (lineage III)
Czech Republic (18): 1 ♂* (SMMZ 6713 [S]), Baštův mlýn Mill, Havraníky (Znojmo Dist.), 29 June 2001, leg. A. Reiter; – 1 ♂* (NMP 94582 [S+A]), Klíčava, mine (Rakovník Dist.), 17 August 2006, leg. R. Lučan; – 2 ♂♂*, 2 ♀♀* (NMP 94571–94574 [S+A]), Ledové sluje Caves, Čížov (Znojmo Dist.), 1 September 2006, leg. P. Benda and A. Reiter; – 1 ♀* (NMP 94575 [S]), Ledové sluje Caves, Čížov (Znojmo Dist.), 16 July 2007, leg. P. Benda and A. Reiter; – 2 ♂♂* (NMP 94578, 94579 [S+A]), Ledové sluje Caves, Čížov (Znojmo Dist.), 10 July 2008, leg. P. Benda and A. Reiter; – 1 ♂*, 1 ♀* (NMP 94580, 94581 [S+A]), Líšná (Přerov Dist.), 9 September 2008, leg. R. Lučan; – 1 ♂* (NMP 94583 [S+A]), Smrdutá Reserve, Chvalčov (Kroměříž Dist.), August 2006, leg. R. Lučan; – 1 ♂* (NMP 94587 [S+A]), Tvořihráz (Znojmo Dist.), 2 August 2006, leg. A. Reiter; – 1 ♂* (NMP 94586 [S+A]), Vlkov Pond, Šumná (Znojmo Dist.), 1 August 2007, leg. A. Reiter; – 2 ♀♀* (NMP 94569, 94570 [S+A]), Vůznice Reserve, Nižbor (Rakovník Dist.), date unlisted, leg. R. Lučan; – 1 ♂*, 1 ♀* (NMP 94576, 94577 [S+A]), Vůznice Reserve, Nižbor (Rakovník Dist.), 15 August 2006, leg. R. Lučan. – **Greece** (3): 1 ♀* (OHC unnumbered [S]), Arkoudorema (Drama Dist.), 18 August 1997, leg. O. von Helversen; – 1 ♂* (OHC unnumbered [S]), Loutropygi (Kardits Dist..), 5 June 1991, leg. K.-G. Heller and M. Volleth; – 1 ♀* (OHC MV336 [S+B], paratype of *Myotis alcathoe* von Helversen et Heller, 2001), Loutropygi (Karditsa Dist.), 17 June 1992, leg. O. von Helversen. – **Montenegro** (1): 1 ♀* (NMP 90228 [S+A]), Plužine, 8 August 2002, leg. P. Benda. – **Romania** (1): 1 ♂* (MHNG 985.16 [S+B]), Olténie, Avenul 2din Sohodoale, January 1961, leg. A. Burghele. – **Slovakia** (4): 1 ♂*, 1 ♀* (NMP 94576, 94577 [S+A]), Boťany (Trebišov Dist.), 21 July 2007, leg. P. Benda & Š. Danko; – 1 ♂*, 1 ♀* (NMP 50446, 50447 [S+A]), Stĺpová Cave, Šurice (Rimavská Sobota Dist.), 8 August 2001, leg. P. Benda & M. Uhrin. – **Switzerland** (1): 1 ♀* (MHNG 1828.073 [S+A]), Arzier (Vaud Prov.), 9 September 2002, leg. M. Ruedi.

Myotis alcathoe ssp. (lineage IV)
Russia (21): 1 ♀ (ZIN 69582 [S+A]), Aše (Černomorskaâ Guberniâ [= Krasnodar Prov.]), 20 July 1913, collector unlisted; – 1 ♂*, 1 ♀* (NMP 95329, 95330 [S+A]), Aše (Krasnodar Prov.), 21 August 2007, leg. S. Gazarân; – 1 ♂* (NMP 95309 [S+A]), Bol'šaâ Fanagorijskaâ Cave, Fanagorijskoe (Krasnodar Prov.), 3 October 2007, leg. S. Gazarân; – 5 ♂♂* (NMP 95324–95328 [S+A]), Bol'šaâ Fanagorijskaâ Cave, Fanagorijskoe (Krasnodar Prov.), 30 September 2008, leg. S. Gazarân; – 5 ♀♀* (NMP 95313–95317 [S+A]), Gebeus Mt., Gešebs (Krasnodar Prov.), 11 July 2007, leg. S. Gazarân; – 1 ♀ (ZMMU S10447 [S+A]), Gelendžik, Black Sea Coast [Krasnodar Prov.], 20 August 1927, leg. B. Obrazcov; – 1 ind. (ZMSO 263 [S+A]), Hosta River, Kavkazskij Reserve [Krasnodar prov.], 8 July 1967, collector unlisted; – 2 ♀♀* (NMP 95307, 95312 [S+A]), Psekabs River, Thamaha (Krasnodar Prov.), 24 May 2008, leg. S. Gazarân; – 1 ♂* (NMP 95331 [S+A]), Tahira Cave, Kalež (Krasnodar Prov.), 22 August 2007, leg. S. Gazarân; – 1 ♀* (NMP 95306 [S+A]), Utriš Peninsula (Krasnodar Prov.), 27 June 2007, leg. S. Gazarân; – 1 ♀ (ZIN 6031 [S+A]), Vladikavkaz [North Ossetia Prov.], 1896, collector unlisted. – **Turkey** (2): 1 ♀ (NMW 30707 [S+A]), Kartschal Gebirge, südlich von Batum [= Kaçkar Dağı Mts., Artvin Prov.], 1896, leg. A. Hacker; – 1 ♂ (OHC [unnumbered] [S]), Şohun Dere (Erzurum Prov.), 8 August 1983, leg. O. von Helversen.

Myotis hyrcanicus (lineage V)
Iran (1): 1 ♂* (NMP 90857 [S+A]; holotype of *Myotis hyrcanicus* Benda, Reiter et Vallo, 2012), Korud Abad, near Ali Abad (Golestan Prov.), 28 May 2006, leg. P. Benda and A. Reiter.

Myotis brandtii (lineage VI)
Crimea (1): 1 ♂* (NMP pb4345 [S+A]), Partizanskoe (Âlta Dist.), 16 September 2009, leg. S. Gazarân. – **Georgia** (1): 1 ♂ (ZIN 9253 [S+A]), Bakuriani (Tiflisskaâ Guberniâ) [Samche-Džavaheti Prov.], 9 July 1910, leg. K. Satunin. – **Russia** (7). 1 ♂* (NMP 95310 [S+A]), Dzyhra Lake, Ahštyr' (Krasnodar Prov.), 13 August 2002, leg. S. Gazarân; – 2 ♀♀ (ZIN 23490, 23491 [S+A]), Kavkaz [= Caucasus Mts.], date unlisted, leg. Gorbunov; – 1 ♂ (ZIN 9260 [S+A]), Psebaj (Kubanskaâ Oblasť) [Krasnodar Prov.], date and collector unlisted; – 1 ♂, 1 ♀ (ZIN 78286, 78287 [S+B]), Pšiš River, between Oktjabrskij and Kurinskij villages (Krasnodar Prov.), 30 May 1990, leg. P. Strelkov; – 1 ♂ (ZIN 80876 [S+B]), Teberda River, Teberda (Karačaevo-Čerkessia Prov.), 8 June 1994, leg. P. Strelkov. – **Turkey** (4): 3 ♀♀ (ZDNU

2001/124–126 [S+B]), Çamlıhemşin, Çat (Rize Prov.), 24 August 2001, leg. A. Karataş; – 1 ♀ (ZDNU 2002/23 [S+B]), Hacıbekir Farm, Çeşka Ruins (Yozgat Prov.), 12 April 2002, leg. H. Öztekin.

M. davidii (lineage II)
Azerbaijan (7): 1 ♀ (NMP 49237 [S+B]), Acınohur, steppe, 27 June 1986, coll. V. Hanák; – 2 ♀♀ (ZIN 9018, 9019 [S+A]), Elizavetpol'skaâ Guberniâ [= Gănčă Prov.], 1895, leg. K. Satunin; – 2 ♀♀ (ZIN 23506, 23507 [S+A]), Geok-Tapa Arešskogo uezda, Elizavetpol'skaâ Guberniâ [=Ağdaş, Ağdaş Dist.], 30 July 1915, leg. K. Satunin; – 1 ind. (ZIN 5346 [S+A]), Kura River, Salyan [Salyan Dist.], 1888, collector unlisted; – 1 ♀ (NMP 48521 [S+B]), Şəki Dist., 29 April 1976, leg. I. K. Rahmatulina. – **Crimea** (18): 1 ind. (ZIN 49554 [S]), Crimea, 26 June 1916, collector unlisted; – 1 ♂ (ZIN 45249 [S+B]; holotype of *Myotis mystacinus popovi* Strelkov, 1983), Kamenskoe, Kerčenskij Peninsula [Lenino Dist.], February 1961, leg. A. Konstantinov; – 2 ♂♂*, 1 ♂ (NMP pb4406–4408 [S+A]), Kamenskoe (Lenino Dist.), 17 September 2009, leg. P. Benda, S. Gazarân and M. Uhrin; – 2 ♂♂ (ZIN 68508, 68509 [S]), Karadag, Crimea [Feodosiâ Dist.], June–July 1916, collector unlisted; – 3 ♂♂ (ZIN 9249–9251 [S+B], paratypes of *Myotis mystacinus popovi* Strelkov, 1983), Simferopol' vicinity [Simferopol' Dist.], 1889, collector unlisted; – 2 ♂♂*, 4 ♂♂ (NMP pb4354–4358 [S+A], NMP pb4359 [A]), Suuk-Koba Cave, Čatyr-Dag Âjla (Simferopol' Dist.), 22 September 2009, leg. P. Benda, S. Gazarân and M. Uhrin; – 2 inds. (ZIN 8057, 9189 [S+B], paratypes of *Myotis mystacinus popovi* Strelkov, 1983), Tatajkoj, Crimea [= Fersmanovo, Simferopol' Dist.], 1890, collector unlisted. – **Georgia** (1): 1 ♂ (ZIN 9287 [S+A]), Lagodehi [Kakheti Dist.], 25 July 1911, leg. K. Satunin. – **India** (1): 1 ♀ (BMNH 26.3.1.1. [S+B]; holotype of *Myotis meinertzhageni* Thomas, 1926), Nubra and Shiyok rivers junction, Ladak [Jammu and Kashmir State], 17 June 1925, leg. R. Meinertzhagen. – **Iran** (4): 1 ♀ (HMNH 2007.30.3. [S+A]), Ahmad Beiglu (Ardabil Prov.), 18 July 2006, leg. E. Sheikh-Jabbari and H. Sheikh-Jabbari; – 2 ♂♂* (NMP 48119, 48120 [S+A]), Bastam (Azarbaijan-e Gharbi Prov.), 30 September 1998, leg. M. Andreas, P. Benda, A. Reiter and M. Uhrin; – 1 ind. (NMP 93914 [S+Sk]), Qutur Su (Ardabil Prov.), 31 August 2010, leg. K. Faizolahi. – **Russia** (22): 1 ♂* (NMP 95308 [S+A]), Apšeronsk (Krasnodar Prov.), 20 July 2008, leg. S. Gazarân; – 3 ♂♂* (NMP 95318–95320 [S+A]), Egerskaâ Karaulka (Adygea Prov.), 8 August 2005, leg. S. Gazarân; – 1 ♀ (ZIN 69879 [S+B]), railway quarters near Ipatovo (Stavropol' Prov.), 4 July 1983, collector unlisted; – 1 ♂ (ZIN 83623 [S+B]; holotype of *Myotis mystacinus caucasicus* Tsytsulina, 2000), Kiša forestry, Caucasus Reserve (Krasnodar Prov.), 19 June 1998, leg. B. Tuniev; – 1 ♀ (ZMMU S166219 [S+A]), Krinipovskoe, Tuapse Dist. (Krasnodar Prov.), 10 August 1998, leg. S. Kruskop and S. Apisimova; – 2 ♀♀* (NMP 95302, 95303 [S+A]), Kumtor-Kala Station (Dagestan Prov.), 22 June 2005, leg. S. Gazarân; – 1 ♂ (ZMMU S9266 [S+B]; holotype of *Myotis mystacinus aurascens* Kuzâkin, 1935), Kurkužin near Vladikavkaz, Southern Caucasus [North Ossetia Prov.], 11 May 1928, leg. A. Radyŝev; – 2 ♀♀ (ZMMU S46560, S46562 [S+B]), Kurkužin near Vladikavkaz [North Ossetia Prov.], 11 May 1928, leg. A. Radyŝev; – 3 ♀♀ (ZIN 80847, 80848, 80850 [S+B]), road between Levokumskoe and Aleksandrovskoe (Stavropol' Prov.), 15 June 1994, leg. P. Strelkov; – 1 ♀ (ZIN 78274 [S+B]), Malyj Irtyš Field Base, Novorossijsk Dist. [Krasnodar Prov.], 17 August 1990, leg. P. Strelkov; – 1 ind. (ZIN 4910 [S]), Mius Dist. [Dagestan Prov.], date and collector unlisted; – 1 ♂ (ZIN 83771 [S+A], paratype of *Myotis mystacinus caucasicus* Tsytsulina, 2000), ca. 10 km E of Psebaj, Ahmet-skala Range (Krasnodar Prov.), January 1998, leg. S. Gazarân; – 1 ind. (ZMMU S5022 [S+B]), Tarasov Dist. (Rostov-na-Done Prov.), 14 September 1926, collector unlisted; – 1 ♂ (ZMMU S29432 [S+B]), Tarasovka Station (Krasnodar Prov.), 17 August 1925, leg. V. Raevskij; – 1 ♀ (ZIN 78288 [S+B]), Terek River, Kargaminskaâ, Groznyj–Kizlâr road [Čečnâ Prov.], 6 June 1990, leg. P. Strelkov; – 1 ♀ (ZMMU S166220 [S+A]), Tuapse Dist. (Krasnodar Prov.), 12 August 1998, leg. S. Kruskop and S. Apisimova; – 1 ♂ (ZMMU S46564 [S]), North Caucasus, 2 May 1928, leg. A. Radyŝev. – **Tajikistan** (1): 1 ♀ (ZMMU S9265 [S]; holotype of *Myotis mystacinus pamirensis* Kuzâkin, 1935), Âšil'-kul Lake, Pamir Mts. [Gorno-Badahšan Prov.], 27 August 1934, leg. R. Meklenburcev. – **Turkey** (22): 1 ♂ (NMW 20644 [S+B]), Agzikarahan (Niğde Prov.), 18 July 1975, leg. F. Spitzenberger; – 2 ♂♂ (NMW 34377, 34378 [S+B]), Akdamar Island, Van Lake (Van Prov.), 18 July 1984, leg. F. Spitzenberger; – 1 ♀, 2 inds. (ZIN 9002, 9003, 9009, 9011 [S+A]), Aralyh (Erivan'skaâ Guberniâ) [= Aralık (Iğdır Prov.)], 6 September 1910, leg. K. Satunin; – 1 ♂, 1 ♀ (ZDNU 1998/101, 103 [S+B]), Beyşehir (Konya Prov.), 9–10 August 1998, leg. A. Karataş; – 1 ♂ (NMW 34379 [S+B]), Eski Van (Van Prov.), 20 July 1984, leg. F. Spitzenberger; – 1 ♂ (OHC unnumbered [S+B]), a valley NW of Ispir (Erzurum Prov.), 4 August 1983, leg. O. von Helversen; – 1 ♀ (NMW 34375 [S+B]), Komus deresi (Bitlis Prov.), 16 July 1984, leg. F. Spitzenberger; – 2 ♂♂, 2 ♀♀ (NMW 37205–37208 [S+B]), Sardes in Sartmustafa (Manisa Prov.), 21 August 1986, leg. F. Spitzenberger; – 1 ♀ (ZDNU 2003/38 [S+B]), Sarıkamış, 2 km S of Sirbasan (Kars Prov.), 21 July 2003, leg. A. Karataş and F. Toprak; – 1 ♂ (ZDNU 2000/15 [S+B]), Selim, Sarıgün (Kars Prov.), 15 September 2000, leg. A. Karataş; – 1 ♂ (NMP 48094 [S+A]), a railway bridge ca. 5 km N of Sirbasan (Kars Prov.), 10 September 1995, leg. P. Benda and I. Horáček; – 1 ♀ (OHC unnumbered [S+B]), Taurus Mts. near Üçpınar, ca. 20 km E of Bozkir (Konya Prov.), 27 June 1986, leg. O. von Helversen; – 1 ♀ (NMW 34380 [S+B]), ENE of Tercan (Erzincan Prov.), 24 July 1984, leg. F. Spitzenberger; – 2 ♂♂ (NMP 47913, 47914 [S+A]), Van Castle (Van Prov.), 28 July 1992, leg. P. Benda. – **Turkmenistan** (1): 1 ♂ (ZMMU S29214 [S+B]; holotype of *Myotis mystacinus transcaspicus* Ogneff et Heptner, 1928), Germab, Kopetdagh Mts., Zakaspijskaâ Oblast' [Ahal Prov.], 12 June 1925, leg. S. Ognev. – **Ukraine [s.str.]** (5): 1 ♂ (ZIN 49555 [S+B]), Bolgrad (Melitopol' Prov.), 5 August 1913, collector unlisted; – 1 ind. (ZMMU S29157 [S], paratype of *Myotis mystacinus popovi* Strelkov, 1983), Doneck Prov., 31 August 1926, leg. N. Kalabuhov; – 1 ♂, 2 ♀♀ (ZIN 78275–78277 [S+B]), Kujuk-Tuk Island, Sivaš Bay (Herson Prov.), 12–13 August 1990, leg. P. Strelkov. – **Uzbekistan** (1): 1 ♀ (ZMMU S6819 [S]; holotype of *Myotis mystacinus sogdianus* Kuzâkin, 1934), Taškent [Tošken Prov.], 14 September 1932, leg. A. Kuzâkin.

M. hajastanicus
Armenia (18): 2 ♀♀ (ZIN 82449, 82450 [S+A]), Aparan, Sevan Lake, 9 August 1973, leg. E. Âvruân; – 2 ♀♀ (ZIN 82441, 82442 [S+A]), Basargečar near Karčahpûr, 6 July 1973, leg. E. Âvruân;

– 3 ♀♀ (ZIN 82443–82445 [S+A]), Čkalovka, Sevan Lake, 17 September 1973, leg. E. Âvruân; – 1 ♀ (ZIN 9008 [S]), Erivan', August 1902, collector unlisted; – 1 ind. (ZIN unnumbered [S]), Sevan Lake, date and collector unlisted; – 2 ♀♀ (NMP 48536, 48537 [S+B]; paratypes of *Myotis mystacinus hajastanicus* Argiropulo, 1939), Šordža, eastern bank of the Sevan Lake, 25 June 1928, leg. A. Šelkovnikov; – 2 ♀♀ (ZMMU S104453, S104454 [S]), Šordža, Gokča [= Sevan] Lake, 20 April 1932, leg. A. Šelkovnikov; – 5 ♀♀ (ZIN 82436–82438 [S], 82439, 82440 [S+A]), Šordža, Sevan Lake, 11 August 1972, leg. E. Âvruân.

Appendix 2.2. List of unidentified specimens.

Azerbaijan (3): 1 ♀, 1 ind. (ZIN 8182, 76-1916 [S]), Geok-Tapa Arešskogo uezda, Elizavetpol'skaâ Guberniâ [= Ağdaş, Ağdaş Dist.], 1906, 30 July 1915, leg. K. Satunin; – 1 ♂ (NMP 48519 [S+B]), Göyçay [İsmaıllı Dist.], 29 August 1975, ded. V. Hanák. – **Russia** (4): 1 ♂ (ZIN 5721 [S]), Astrahan' [Astrahan' Prov.], 1877, collector unlisted; – 1 ♂ (ZIN 4909 [S]), Mius (Dagestan Prov.), date and collector unlisted; – 1 ♂ (ZIN S46565 [S]), Nal'čik [Kabardino-Balkaria Prov.], 23 August 1928, leg. A. Radyŝev; – 1 ♂ (ZMMU 46561 [S]), Southern Caucasus, 31 May 1925, leg. A. Radyŝev. – **Turkey** (7): 1 ♂, 1 ♀ (ZIN 9002, 9012 [S]), Aralyh, Elizavetpol'skaâ guberniâ [= Aralık, Iğdır Prov.], 1901, 6 September 1906, leg. K. Satunin; – 1 ♀ (OHC unnumbered [S+B]), Beşkonak (Antalya Prov.), 10 October 1984, leg. O. von Helversen; – 1 ♂, 1 ♀ (ZDNU 2001/86, 2002/111 [S]), Kirmir River, Kızılcahamam (Ankara Prov.), 30 July 2001, 8 August 2002, leg. A. Karataş; – 1 ♂ (NMP 48095 [S+A]), Sirbasan (Kars Prov.), 10 September 1995, leg. P. Benda and I. Horáček; – 1 ♂ (NMP 47912 [S+A]), Van Castle (Van Prov.), 28 July 1992, leg. P. Benda.