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SYNONYMISATION OF *MYOTIS AURASCENS* WITH *M. DAVIDII* (CHIROPTERA, VESPERTILIONIDAE) IS PREMATURE

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Synonymisation of *Myotis aurascens* with *M. davidii* (Chiroptera, Vespertilionidae) is Premature. Dzeverin, I. — Based on morphological and molecular data Benda et al. (2012) suggested that East European and West and East Asian steppe whiskered bat, *Myotis aurascens* Kuszajkin, 1935, is conspecific to *M. davidii* (Peters, 1869) described from China. This hypothesis found considerable support and eventually it may even turn out to be true, but at present it still needs more testing. It is only clear so far that the steppe whiskered bats from the western Eurasia and steppe whiskered bats from southern China are different, phylogenetically quite distant species. The study of variation and between-group differences of the steppe whiskered bats in morphological characters and molecular markers throughout the species geographic range is needed, and especially the comparison of their molecular genetic traits with those of *M. davidii* from the type locality (Beijing). Until such an analysis is done, taxonomic statements on the synonymy of the names *M. aurascens* and *M. davidii* are premature.

Key words: *Myotis*; *Myotis aurascens*, *Myotis davidii*, *Myotis alticraniatus*, taxonomy, nomenclature.

Introduction

The steppe whiskered bat, *Myotis aurascens* Kujakin, 1935 (Vespertilionidae, Chiroptera, Mammalia), is a common widespread bat species with complex taxonomic structure. The species status was substantiated for this bat by Benda & Tsytsulina (2000). Earlier (see Benda & Tsytsulina, 2000 : 362 for complete references), *Myotis aurascens* was considered to be a subspecies or synonym of *Myotis mystacinus* (Kuhl, 1817). Since Benda & Tsytsulina (2000) showed that these two taxa are to be considered well separated species, *M. aurascens* was suggested to be a species that comprises a number of more or less distinct subspecific operational taxonomic units (OTUs) and distributed from the Balkans to Korea that is one of the broadest geographic ranges among the Palaearctic bat species (Tsytsulina et al., 2012).

Later, Benda et al. (2012) suggested that East European and West and East Asian steppe whiskered bat *M. aurascens* is conspecific to *M. davidii* (Peters, 1869), a bat species from China (Benda et al., 2012: 333–334). Should this point of view be correct, then the name *M. davidii* is the senior synonym of *M. aurascens*, and the latter name should be considered a junior synonym or may be used as the subspecies name *M. davidii aurascens* among other numerous subspecies of *M. davidii*. Several researchers agreed with this concept (e. g., Kruskop et al., 2018; Çoraman et al., 2020; Ruedi et al., 2021); moreover, the Meeting of the Parties to the Agreement on the Conservation of Populations of European Bats decided to add *M. davidii* on the list of bat species occurring in Europe to which the Agreement applies and to remove *M. aurascens*, *M. nipalensis* and *M. hajastanicus* from this list as synonyms of *M. davidii* (Hutson, 2018; Resolution 8.2, 2018). Taxonomic status of *Myotis nipalensis* (Dobson, 1871) and *Myotis hajastanicus* Argyropulo, 1939 remains unclear; they are usually treated as the sibling species or subspecies of *M. aurascens* or *M. davidii* (e. g., Benda et al., 2012; Dietz et al., 2016; Ruedi et al., 2021).

The Problem

Benda et al. (2012) base the hypothesis of conspecificity of *M. aurascens* and *M. davidii* on (i) morphometric data (Benda et al., 2012: 329, table 16) and scatter plots based on them (Benda et al., 2012: 330, figs 95, 96); (ii) outlines of skulls and the elements of the dental system of the specimens of several whiskered *Myotis* OTUs (Benda et al., 2012: 332, 333, figs 97, 98); (iii) the phylogeny reconstruction based on the cytochrome *b* sequences (Benda et al., 2012: 335, table 17) and a tree built on the basis of these data (Benda et al., 2012: 333, fig. 99).

Benda et al. (2012: 329, table 16) provided the morphometric data of nine specimens: four *M. mystacinus* s. str., four *M. davidii* from Iran (i. e., *M. aurascens* in the previous classification by Benda & Tsytsulina (2000)) and a type specimen of *M. davidii* from Beijing.

The scatter plots given by Benda et al. (2012: 330, figs 95, 96) show that the Iranian specimens are markedly different from *M. mystacinus* s. str., and that the type specimen of *M. davidii* is much closer to them than to *M. mystacinus* s. str.

At the same time, the type specimen of *M. davidii* in some characters falls into the area of Iranian specimens on the plot (fig. 1, A–D in the present paper). In other characters it does not fall into this area, but is at a place close to this area, being smaller in most characters than Iranian specimens (fig. 1, A, C). In some additional characters, *M. davidii* is intermediate between the Iranian sample and *M. mystacinus* s. str. sample (fig. 1, B, D). Since variation patterns seem to be different for different characters, skull shape can differ in the studied OTUs. These differences do not refute the conspecificity of Iranian and Chinese steppe whiskered bats (differences are expected for populations living in geographically remote and ecologically different localities), but also they cannot be evidence in support of this hypothesis.

The name-bearing type specimen of *Vespertilio davidii* has not been compared with the type specimens of *aurascens*, *popovi*, *sogdianus*, and a number of other OTUs (possibly, subspecific) of the steppe whiskered bat (while some other type specimens are shown in the

plots). In addition, samples of only four specimens are insufficient when such a complex group of taxa as the *M. mystacinus* complex, which comprises a number of OTUs with considerable between- and within-group variation is studied.

At most we can say from the morphometric data provided by Benda et al. (2012) that the studied Iranian steppe whiskered bats are more similar to the *M. davidii* type specimen than to the studied *M. mystacinus* s. str. sample in a number of characters.

Almost the same can be said about the drawings of *Myotis* skulls (Benda et al., 2012: 332, fig. 97) and teeth (Benda et al., 2012: 333, fig. 98). Benda et al. (2012) demonstrated four skull and teeth outlines: for *M. mystacinus* s. str., the type specimen of *M. hyrcanicus*, the steppe bat from Iran (*M. davidii* according to the classification of Benda et al.; *M. aurascens* according to the previous classification), and the type specimen of *M. davidii*. The sample is hardly sufficient: the skull is a diverse and variable structure, both divergent and convergent evolutionary shifts are possible in its size and shape, at least it is needed to compare the skulls of a larger number of OTUs and take into account the within-group variation, particularly geographical, in skull and teeth size and shape for each of the OTUs under analysis.

The results of Bayesian inference analysis among the haplotypes within the *Myotis mystacinus* morpho-group (complete cytochrome b sequences) provided by Benda et al. (2012: fig. 99) show that the three haplotypes from the specimens collected in Eastern Kazakhstan, Tiva and South Korea form a clade, separate from the other terminal taxa of *Myotis aurascens* sensu Benda & Tsytsulina (2000), but only with pairwise genetic distances varying between 3.6–6.6, which is less than half the distances between Iranian *M. mystacinus* and Iranian *Myotis aurascens* sensu Benda & Tsytsulina (Benda et al., 2012: 337, table 18). This shows that differences between the Western and the Eastern (to which the type of *M. davidii* is believed to belong) populations of *Myotis aurascens* are of at most subspecies level. Later, such a subdivision was generally confirmed and substantiated by Çoraman et al. (2020; see below for more details).

Discussion

The traditional view on the bat species *M. davidii* is based on the study of a few, apparently only three specimens (including holotype) from Beijing and southern China (Peters, 1869: 402; J. A. Allen, 1906: 488; Howell, 1929: 15; G. M. Allen, 1938: 223).

There is no universally accepted understanding of the morphology of this species. The *Myotis* genus includes large species groups with similar morphological and ecological characters that were previously considered to be subgenera, and are now considered to be ecomorphs, namely ‘*Myotis*’, ‘*Selysius*’, and ‘*Leuconoe*’ (Findley, 1972; Ruedi and Mayer, 2001). Usually *M. davidii* is treated as a representative of the subgenus *Selysius* (Findley, 1972: 42) or ‘*Selysius*’ ecomorph (modern authors, e. g. Ghazali et al., 2017) as well as *M. mystacinus* and *M. aurascens*. Surprisingly some older authors attributed this species to ‘*Leuconoe*’ rather than ‘*Selysius*’. Howell (1929: 15) emphasized that *M. davidii* is similar to *M. daubentonii*; the latter bat is typical ‘*Leuconoe*’ and is markedly different from the ‘*Selysius*’ bats. Tate pointed out the resemblance of the supposed specimen of *M. davidii* to *M. daubentonii*, noted that *M. davidii* characters are characteristic for *Leuconoe*, and assigned this species to a separate section within this subgenus in his classification of *Myotis* (Tate, 1941: 542, 551).

In the description of the species he discovered, Peters mentioned some external characters, as well as the characters of the dental system: “Der obere und untere zweite Prämo-

larzahn sind ganz aus der Reihe heraus nach innen gedrängt und sehr klein und die inneren aus dem Cingulum hervorgehenden Zacken der backzähne, welche bei *V. mystacinus* so spitz und sehr entwickelt sind, sind hier nur als stumpfe Höcker vorhanden” (my translation from German is: “The upper and lower second premolars are crowded in entirely out of line and very small, and the inner cusps of the molars, arising from the cingulum, which are so acute and very developed in *V. mystacinus*, are present here only as blunt cusps”) (Peters, 1869: 403). “*V. mystacinus*” here seems to be *M. mystacinus* in the broadest sense, including *M. brandtii*, *M. aurascens* and a number of other more or less similar OTUs.

It is not clear why Benda et al. (2012) used only upper unicuspidal teeth (Benda et al., 2012: 333, fig. 98). It would be worthwhile to use other teeth in the revision, e. g. molars, both upper and especially lower ones. Teeth of various types are important for phylogenetic and taxonomic studies (Menu, 1985, 1987), particularly for *M. mystacinus* s. l. (Benda & Tsytulina, 2000).

In addition, regarding the premolars, Peters and other authors unanimously noted internal position and high degree of decreasing the upper second premolars (P^3 , according to comparative anatomical notation). J. A. Allen (1906: 488) noted “the small size and internal position of the second premolar in both jaws” of *M. davidii*. Howell (1929: 15) found that in *M. davidii*, “second premolar, both above and below, is internal and excessively crowded”. G. M. Allen also mentioned: “The skull is characterized by the position of the small second premolar internal to the tooth row in each jaw, so that the upper first and third premolars are closely approximated, but in the lower jaw separated by a slight space” (Allen, 1938: 223). Such character states look like the character states of P^3 known for eastern populations of *M. mystacinus* s. l. (Strelkov, 1983), later attributed to *M. aurascens*. Teeth of *M. aurascens* and *M. davidii* shown by Benda et al. (2012: 333, fig. 98) are really similar. However, P^3 is vestigial in *Myotis* and therefore highly variable (Menu, 1985: 98–100; Benda & Tsytulina, 2000: 341–342, table 1; Dzeverin, 2001, 2007). The regressive evolution of P^3 (size decreasing, displacement from the toothrow, increasing variation) occurred in a number of *Myotis* lineages, and similar character states could have arisen in different species (Dzeverin, 2001, 2007). Increased variation of P^3 is well known for *M. mystacinus* s. l. (Strelkov, 1983; Ghazali & Dzeverin, 2004), moreover, within the species this variation shows partly geographical pattern (Strelkov, 1983; Benda & Tsytulina, 2000). Sometimes, vestigial structures mark taxa or regional groups and thus can be used in taxonomy but caution is needed if they are used due to their simplification and increased variation.

The analysis of cytochrome *b* sequences showed that the haplotypes of steppe whiskered bats from many regions (Moldova, Ukraine, Russia: the northern Caucasus and the Volga region, Iran, Turkmenistan, Kazakhstan, Kyrgyzstan, South Korea) are very similar, so that all these bats can be considered as representing the same species (Benda et al., 2012: 334–335, fig. 99, table 17). This analysis includes no sequences obtained from specimens collected in Beijing, the type locality of *M. davidii*, and does not support the taxonomic and nomenclatural inferences of Benda et al. (2012) directly.

Additional *M. davidii* specimen (from Guangzhou, Guangdong, China) used in the molecular analysis by Benda et al. (2012) is rather distant from other *M. davidii* specimens (as well as from other *M. mystacinus* s. l. specimens) in the phylogenetic tree as far as can be seen from fig. 99 (Benda et al., 2012: 334). For that specimen, Benda et al. (2012) put the species name in quotation marks – *M. “davidii”* – probably to emphasize that the assignment of this specimen to *M. davidii* is dubious. The authors comment the status of the populations, from which this specimen had evidently been obtained, as follows: “Another

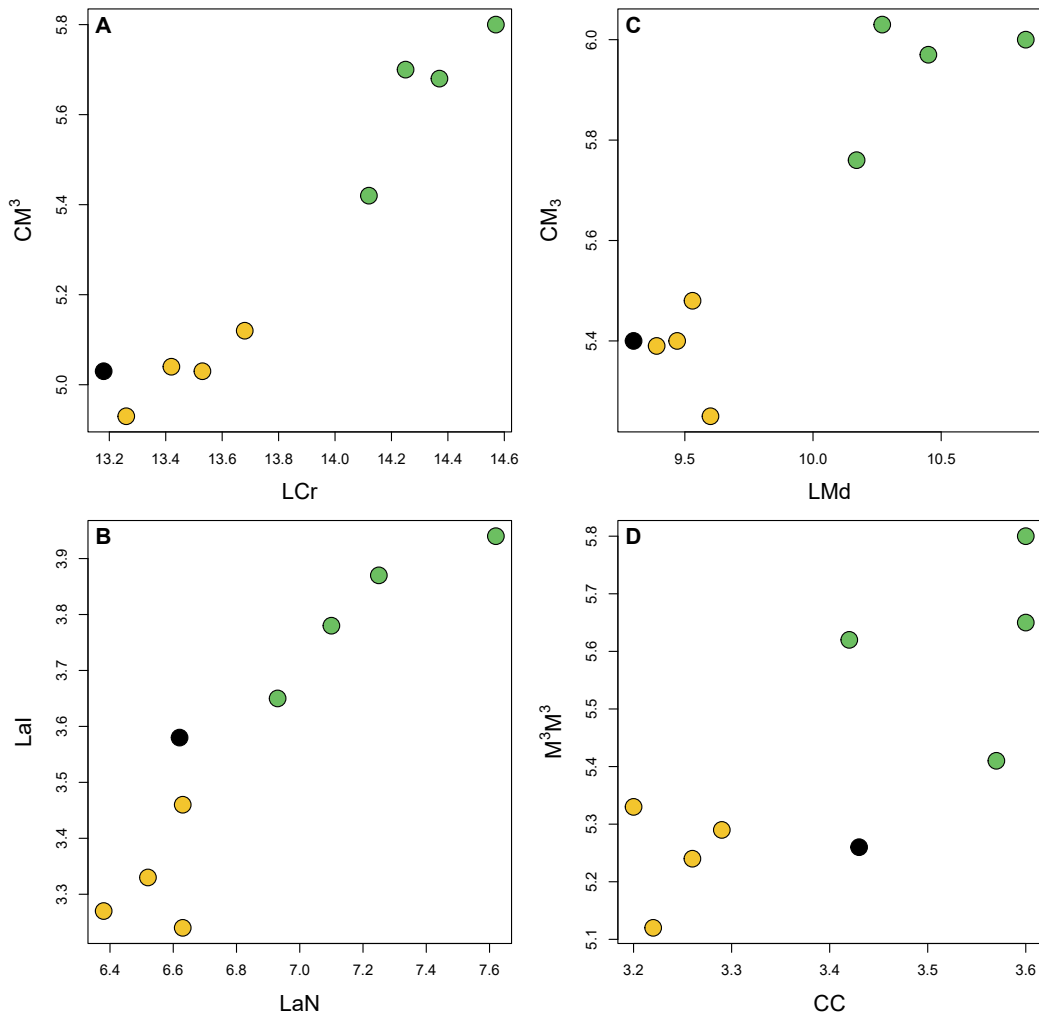


Fig. 1. Bivariate plots of the *Myotis* samples listed by Benda et al. (2012) to demonstrate the correspondence of Iranian steppe whiskered bats with *M. mystacinus* s. str. and *M. davidii*. LCr is the greatest length of skull; LMd is condylar length of mandible; CM³ is length of upper tooththrow between C and M³ (incl.); CM₃ is length of lower tooththrow between C and M₃ (incl.); LaI is width of interorbital constriction; LaN is neurocranium width; CC is rostral width between canines (incl.); M³M³ is rostral width between the third upper molars (incl.). The measurements are in mm. All measurements are from Benda et al. (2012: 329, table 16). Fig. 1, A partly repeats Fig. 95 of Benda et al. (2012: 330), however Benda et al. also added the data given by DeBlase (1980) to this figure as well as to fig. 96. *M. mystacinus* s. str. specimens are shown in green; *M. aurascens* specimens from Iran attributed by Benda et al. (2012) to *M. davidii* are shown in yellow; type specimen of *M. davidii* is shown in black. See Benda et al. (2012: 329, table 16) for more details about these specimens. The figure was obtained using R software (R Core Team, 2021).

question is the actual taxonomic position of the populations of small-sized *Myotis* assigned to *M. davidii* by some Far Eastern authors of molecular genetic analyses (see e. g. Kawai et al., 2003, You et al., 2010), which is certainly not linked with the *M. mystacinus* morpho-group (see position of this genotype in results of the *cyt b* analysis; fig. 99)” (Benda et al., 2012: 336). It remains unclear why the authors consider the application of the name *M. davidii* correct to the Iranian, Korean, East European and Central Asian steppe whiskered bats and incorrect to the whiskered bat from Guangzhou, and not vice versa. Further, the authors note: “these problems can be solved only with the help of a broad analysis combin-

ing both morphological and genetic evidence of a large geographical extent and representative sampling” (Benda et al., 2012: 336). It is hard to disagree with this final declaration.

Kawai et al. (2003) and You et al. (2010) used molecular sequences of bats from southern China, but did not question the application of the name *M. davidii* to these populations. Ghazali et al. (2017) also used the sequences of *M. davidii* from Guangdong and, as well as Benda et al. (2012), revealed a considerable difference between this bat and *M. aurascens* from Iran (Ghazali et al., 2017: 477, fig. 1, and also the online supplement to that paper: 7, fig. 2).

Çoraman et al. (2020) showed that steppe whiskered bats from the western part of the range and steppe whiskered bats from Mongolia and Korea are rather similar in nuclear and mitochondrial gene markers, and thus can be considered as the populations from the same species. These authors use *M. davidii* as valid name for this species, however the data on the *M. davidii* from type locality is lacking in their analysis, too. According to Çoraman et al. (2020), the sample of *M. davidii* sensu Benda et al., 2012 comprised two subclades, western (Europe, Caucasus, Kyrgyzstan) and eastern (Mongolia, Korea). Apparently, these clades may be considered as subspecies of the same species or closely related sibling species. If the latter hypothesis is true, then the assignment of the western clade to *M. davidii* occurs to be even more doubtful. Çoraman et al. (2020) assumed that in the case that further studies would identify that these subclades are distinctive at a taxonomic level, then the name “*M. aurascens*” should be recalled to name the western subclade (Çoraman et al., 2020: 11). However, the assignment of the name “*M. davidii*” only to the eastern subclade is also doubtful.

Ruedi et al. (2021) found that all sequences from China available in the GenBank and labeled as “*M. davidii*” certainly represent another species, *M. alticraniatus* Osgood, 1932 (previously considered a subspecies of *M. siligorensis*). Ghazali et al. (2017) also revealed the close relatedness between *M. davidii* and *M. siligorensis alticraniatus*, approximately as between the subspecies of the same species (Ghazali et al., 2017, fig. 1, p. 477, and also the online supplement to that paper: 7, fig. 2). Ruedi et al. (2021) also do not analyze data on *M. davidii* from the type locality. Apparently, these sequences have simply not yet been obtained by the scientists. But while they are not available, we cannot choose between several possible taxonomic solutions.

Hypothetically, it can be assumed that the entire whiskered bat populations from the southern China are erroneously assigned to the species *M. davidii* and actually they are *M. alticraniatus* (and an opposite assumption that not *M. aurascens*, but *M. alticraniatus* is the junior synonym of *M. davidii* also cannot be rejected so far). In the description (Osgood, 1932: 232–234) of the newly discovered subspecies, *M. siligorensis alticraniatus*, Osgood mentioned the size and placement of upper premolars different from those of in *M. davidii*: “anterior upper premolar with a higher crown than a following one, but the diameter of its shaft only slightly greater; small premolars directly in line in the toothrow, separated from the large premolar by a slight space” (Osgood, 1932: 233) as well as a number of other characters that were not noted for *M. davidii*. Meanwhile, J. A. Allen, who described a specimen of *M. davidii* from Hainan Island (southern China) concluded that “this specimen agrees very closely with the description by Peters and Dobson of *M. davidii* (type locality, Peking, China)” (Allen, 1906: 488; Dobson described the color of *M. davidii* — this is mentioned by G. M. Allen, 1938: 223). Allen also noted the larger size and a number of other minor differences between the specimens from Hainan and Beijing and assumed that “it is quite probable that comparison of suitable material from the type locality and from Hainan would show that the Hainan form is entitled to separa-

tion” (Allen, 1906: 488; cf. Allen, 1938: 224). As had been already cited J. A. Allen emphasized the small size and internal position of the second premolar in both jaws of Hainan *M. davidii* specimen (Allen, 1906: 488) that is clearly inconsistent with the description of *M. alticraniatus*.

To distinguish among these OTUs it would probably be useful to apply characters less variable than the size, shape, and placement of vestigial teeth such as P³ (see above). According to Ruedi et al. (2021) *M. alticraniatus* has nyctalodont lower molars that is quite unusual for *Myotis*, which almost all have myotodont molars. Nyctalo- and myotodont configurations of lower molars are highly conservative character states in bats (Menu and Sigé, 1971; Menu, 1985: 119–120). Testing for myoto- vs nyctalodont configuration may seem to be useful in solving the problem under discussion.

It is quite possible that all three species are valid, and that some of the populations considered to be *M. davidii* represent each of these species. But testing can possibly confirm that some OTUs are conspecific. At our present level of knowledge, none of these hypotheses can be discarded. The choice between various possible hypotheses requires studying the geographic variation of *M. davidii* in the eastern part of its range using both morphological characters and molecular markers. All the available published sequences as well as the specimens from the museum collections should be checked for errors and selective choice. It is only clear so far that the steppe whiskered bats from western Eurasia (*M. aurascens* according to the previous classification, *M. davidii* according to the classification of Benda et al., 2012) and steppe whiskered bats from southern China (*M. davidii* according to the previous classification, *M. alticraniatus* according to the classification of Ruedi et al., 2021) are different, phylogenetically quite distant species.

Kruskop et al. (2018: 18, footnote) agreed that the bats previously classified as *M. aurascens* should be treated as *M. davidii*, based on the unpublished results of Kruskop’s work on the type specimen of *M. davidii*. It remains to wait for these results to be published, especially the comparison of this specimen with type specimens of *M. aurascens*, *M. sogdianus*, *M. popovi* and a number of other whiskered bat OTUs. Taking into account new hypotheses, a comparison with type specimens of *M. alticraniatus*, *M. siligorensis*, and possibly some other OTUs seem also to be equally important.

The unresolved problem is that the structure as well as geographic range and variation of *M. davidii* have not been studied, so it remains unclear whether only the northern Chinese populations belong to this species or also some of the southern Chinese ones? Are North Chinese *M. davidii* populations conspecific with *M. aurascens*? In order to answer these questions, it is necessary to study the variation of the discussed populations throughout the range using both morphometric and molecular data. Without this, the taxonomic revisions concerning this species seem to be unfounded. *M. davidii* and *M. aurascens* can be indeed synonyms, or the sympatric species, or vicarious species: different hypotheses are possible here, and each of them needs careful testing. The researcher cannot limit his work to only one of the competing hypotheses. None of these hypotheses can yet be rejected. Benda’s et al. (2012) suggestion seems to be a reasonable working hypothesis and finally it may even turn out to be correct. But the argumentation of Benda et al. is precisely the promotion of a hypothesis, and by no means a comprehensive testing. So far, no strong evidence has been presented for this hypothesis. Therefore, taxonomic statements replacing the name *M. aurascens* with *M. davidii*, such as the conclusion of the working group on the amendment of the annex to the Agreement of the AC to EUROBATS Agreement, adopted by the Meeting of Parties (Hutson, 2018; Resolution 8.2, 2018), seem to be premature.

The status of *M. hajastanicus* and *M. nipalensis* also remains controversial. The conclusion (Hutson, 2018; Resolution 8.2, 2018) that *M. hajastanicus* is conspecific to *M. aurascens/davidii* is based on Dietz et al., 2016, while the conclusion (Hutson, 2018; Resolution 8.2, 2018) that *M. nipalensis* is conspecific to *M. aurascens/davidii* is eventually based on the data and argumentation by Benda et al. (2012). Ruedi et al. (2021) showed that *M. nipalensis* is a species different from *M. davidii*. However, in their analysis the *M. davidii* clade (in the sense close to that of Benda et al., 2012) included the two partial gene sequences previously considered as *M. nipalensis* (Ruedi et al., 2021: 474; cf. Tsytsulina et al., 2012: 18). Therefore, some populations previously identified as *M. nipalensis* can possibly be conspecific to *M. aurascens/davidii*.

It is currently unclear which of the possible hypotheses will be confirmed. E. g., one more hypothesis concerning the steppe whiskered bats taxonomy and nomenclature was suggested by Tsytsulina et al. (2012: 1): “A paratype specimen of the form *sogdianus* Kuzyakin, 1934 appeared in the clade A of *Myotis aurascens*, which suggested clearly that they belong to the same species. However, despite that *sogdianus* Kuzyakin, 1934 should be considered a senior synonym of *aurascens* Kuzyakin, 1935, taking into consideration that a paratype does not have a name-baring function, we do not suggest to make any changes in the species name *Myotis aurascens* till further studies” (Tsytsulina et al., 2012: 1). Of course, this also applies to other names that may occur to be senior synonyms for *M. aurascens* (*M. davidii*, *M. przewalskii*, *M. transcaspicus*, and possibly some others).

Such an approach is believed to be the most correct in the revision of taxa, consistent with the Principle of Nomenclature Stability declared by the International Code of Zoological Nomenclature, and scientific data, and common sense.

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