Taxonomy of the *Myotis frater* species group
(Vespertilionidae, Chiroptera)

Katerina Tsytusulina & Petr P. Strelkov

Abstract. Four subspecies are currently recognised within *Myotis frater* s.l. According to our investigation, *M. bucharensis* is to be considered as a valid species. *M. f. longicaudatus* is represented by two geographically isolated and morphologically distinct forms, one inhabiting the Far East (the type area for *M. f. longicaudatus*) and the other the Krasnoyarsk region in Middle Siberia (*M. f. eniseensis* ssp. nov.).

Key words. *Myotis frater*, taxonomy, new subspecies, East Asia.

Introduction

There are some species groups in *Myotis*, which include taxonomically uncertain forms; one of them is the *Myotis frater* group. Usually these bats can be distinguished from others by highest brain case and great reduction (down to absence) and displacement of the third upper premolar (P3) from the tooth row. However, the last character may also belong to other species groups, e.g. *Myotis mystacinus*.

The Asian longtailed bat – *Myotis frater* – used to be placed into the *Selysius* subgenus, the generally accepted features of which are small feet (less than 50% of tibia), plagiopatagium attached to the base of metatarsus of the first toe, calcar usually possessing a lobe, low rostrum, abruptly rising frontal part of the skull, and usually absent protoconules. Wallin (1969) pointed out that *Myotis frater* should be regarded as a *Selysius* form, though the combination of high, inflated brain case, long tail and tibia and sharp indentation in the posterior border of tragus make it easily distinguishable among other *Selysius* species. A high brain case is also typical of the *Selysius* member *Myotis siligorensis*, which differs from the examined species by smaller body size, not inflated occipit and other details (Hill 1962; Wallin 1969). One of the most principal features of *M. frater*, besides all the above-mentioned ones, is the third upper premolar displaced outside the tooth row. The subspecies rank forms are generally united into *M. frater* on account of this sign, along with inflated brain case.

Four subspecies are currently recognised within *Myotis frater* s.l.: *M. f. frater* Allen, 1923; *M. f. kaguyae* Imaizumi, 1956; *M. f. longicaudatus* Ognev, 1927; *M. f. bucharensis* Kuzyakin, 1950 (Corbet 1978; Koopman 1993, Koopman 1994). Two of them, *M. f. frater* and *M. f. kaguyae*, are Far-East residents (SE China and Japan, respectively), and the other two, *M. f. longicaudatus* and *M. f. bucharensis*, inhabit the former USSR territory. The first one is distributed all over Russian Far East and Middle Siberia (Krasnoyarsk region, Altai), while only two localities were reported for the second one: Aiwadj (SW Tadzhikistan - terra typica) and Samarkand (Uzbekistan) (Fig. 1). All these forms are quite rare, but *M. f. kaguyae* used to be found more frequently.
Materials and Methods

50 adult specimens of *M. frater* s.l. (males and females) have been investigated: 25 alcohol specimens, 9 dry skins and 39 extracted skulls. All measurements were taken with help of electronic calipers.

Abbreviations given in Table 1: External measurements: body length (L), tail length (C), ear length (A), tibia length (Tib), foot length (including claws) (Tars), forearm (Ant), metacarpals (MC) and phalanges of third to fifth digits (fl-3). All wing measurements have been taken from the right wing.

Table 2: Cranial measurements: condylobasal length (CBL), condylocanine length (CCL), width of skull on the level of auditory bullae (W), width of braincase (BCW), height of braincase posteriorly to auditory bullae (BCH), interorbital constriction (IOW), rostral width on the level of preorbital foramen (WR), rostral length from preorbital foramen to alveola of inner incisor (LR), C-M3 length (CM3), length of upper canine cingulum base (LC), width of upper canine cingulum base (WC), length of pseudodiastema (PD), molariform row length (P4M3), width of M3 (WM3), length of M3 (LM3), width between outer margins of upper canines (CC), width between outer margins of M3 (M3M3), lower jaw length from alveole of i1 to articulated process (LMD), lower jaw height to the tip of coronoid process (HMD), length of mandibular tooth row (mCM3).

Specimens taken into analysis, are deposited in the Zoological Institute of Russian Academy of Sciences, St. Petersburg (RAS), Zoological Museum of Moscow State University, Zoological Museum of Irkutsk State University (Irkutsk), Biology & Soil Sciences Institute (Siberian department of Russian Academy of Sciences, Vladivostok) and the American Museum of Natural History (New York).
### Table 1. External measurements of the examined forms (all measurements in mm).

<table>
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<tr>
<th>Species</th>
<th>n</th>
<th>min</th>
<th>max</th>
<th>Mean</th>
<th>SD</th>
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<td>43.00</td>
<td>44.50</td>
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</table>

**Taxonomy of the *Myotis frater* species group**
Table 2. Cranial measurements of the examined forms (all measurements in mm).

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<tr>
<th></th>
<th><strong>Myotis bucharensis</strong></th>
<th><strong>Myotis frater longicaudatus</strong></th>
<th><strong>Myotis frater kagynae</strong></th>
<th><strong>Myotis frater eniseenai</strong></th>
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<tbody>
<tr>
<td></td>
<td>n min max Mean SD</td>
<td>n min max Mean SD</td>
<td>n min max Mean SD</td>
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<td>W</td>
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<td>20 7.30 8.00 7.61 .23</td>
<td>2 7.53 7.76 7.65 .16</td>
<td>6 7.56 8.20 7.79 .22</td>
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<td>BCW</td>
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<td>19 6.86 7.31 7.12 .14</td>
<td>2 6.94 7.31 7.13 .26</td>
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<td>15 5.39 5.74 5.56 .13</td>
<td>2 5.58 5.67 5.63 .06</td>
<td>7 5.45 5.90 5.70 .15</td>
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<td>IOW</td>
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<td>23 3.60 4.30 3.99 .20</td>
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<td>8 4.04 4.40 4.17 .14</td>
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<td>WC</td>
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<td>15 3.05 3.19 3.11 .05</td>
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<td>15 3.70 5.20 4.06 .40</td>
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<td>4 4.00 4.20 4.13 .10</td>
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<td>HM3</td>
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<td>13 3.34 3.81 3.55 .14</td>
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<td>2 5.20 5.40 5.30 .14</td>
<td>3 5.27 5.57 5.40 .16</td>
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</tbody>
</table>
Results

Myotis frater in traditional conception is a complex species and should be divided into several distinct forms, characterised by morphological and ecological characteristics and some peculiarities of their distribution. A detailed diagnosis is presented below for all the above-mentioned forms.

Myotis frater Allen, 1923


Diagnosis. Colour is not evident in the alcohol specimens, but is doubtless dark reddish brown (Allen 1923). Tail is long, about 50% of the total length; ears are short, barely reaching the muzzle when laid forward, tragus is longer than half of the pinna length. Membrane is attached to the base of the outer toe. Skull has short, upturned rostrum, elevated towards forehead (in profile) and slightly inflated brain case (Fig. 2). The upper canines are rounded on cingulum level, and bear two deep grooves on their lingual sides, and one strongly pronounced groove on back-labial sides of upper canines (Fig. 3). The third upper premolar (P3) is quite displaced inward from the tooth row. A metaloph is present on M1 and M2, but no protoconules.

Fig. 2. Two types of the skull profile. Solid line: Myotis bucharensis and M. f. eniseensis ssp. nov.; dashed line: M. f. frater, M. f. longicaudatus, M. f. kaguyae.

The species includes 3 subspecies up to now: M. f. frater Allen, 1923; M. f. longicaudatus Ognev, 1927; M. f. kaguyae Imaizumi, 1961.

Ellerman & Morrison-Scott (1951) include M. f. longicaudatus into M. frater, based on similarity of measurements, which had been published earlier. Wallin (1969) considered it to be well correlated in all characters with M. f. frater and regarded them as synonyms.

In 1956 Imaizumi described M. kaguyae as a distinct species, which was reduced to M. f. kaguyae (Imaizumi 1961) later. Imaizumi primarily compared this form with
Myotis frater. The main differences he mentioned were as follows: tibia and tail much shorter than in M. frater, narrower brain case and longer ears. In connection with the small number of specimens at our disposal we do not presume to speculate about its taxonomic rank and consider it here within M. frater.

Distribution. China (SE China and Heilungkiang), Korea, Japan, Russian Far East (to middle of Khabarovsk region). (Koopman 1993; Koopman 1994; Tiunov, 1984 (Fig. 1). M. f. frater and M. f. kaguyae are seemingly distributed in tropical bamboo forests (Allen 1938; Wallin 1969). M. f. longicaudatus inhabits mixed forests in the plains of southern Far East; occasionally, small groups were found in caves in winter (Tiunov 1984).

Certain differences in external and cranial characters, teeth and baculum shape have been found among M. f. longicaudatus representatives. We consider the form from Middle Siberia a distinct subspecies. It probably may be a distinct species, the confirmation of which would have to be based on more material.

Myotis frater eniseensis ssp. nov.

Holotype. Adult male, No. 59603, skin and skull, Karaulinskiye caves, the left bank shore of the Yenisey river, 18 km from Krasnoyarsk city; November, 7, 1972, collected by Dr. Strelkov; deposited at Zoological Institute RAS, St. Petersburg, Russia.
**Taxonomy of the Myotis frater species group**

**Diagnosis.** Pelage is greyish-brown (from cinnamon brown to Prout's brown by Ridgway 1925). Tail is relatively short, about 95% of body length on average (whereas in *M. f. longicaudatus* tail is always longer than body). Ears are narrow and longer than in other longtailed bats. Tragus is about one half of ear length. Plagiopatagium margin is attached to distal portion of metatarsus of the first toe. Facial portion of skull is shorter than brain case. Rostrum is relatively long, longer than in *M. f. frater*, rising smoothly, and the frontal portion is lower than the occipital one (like in *M. bucharenensis*); brain case is high, slightly inflated (Fig. 2). Upper canines are relatively angular, with two deep grooves on the lingual side, but lacking them on the labial side of the upper canines (Fig. 3). The third upper premolar (P3) (if present) is displaced inward. There is a very low metaloph on M1 and M2 (seemingly be absent on erased teeth) and quite reduced (almost absent) protoconules.

**Distribution.** The largest part of the findings come from Krasnoyarsk region caves: Archeologicheskaya cave (Khakasiya, Shyirinsky district – one adult male, Zoological Institute collection), Ledopadnaya cave (“Stolby” reserve, Krasnoyarsk neighbouring territory – two specimens, Zoological Institute collection, also reported by Khritankov, Melnikova, 1988), Jenevskaya cave (the Birysa river basin – two skulls in Zoological Institute collection) and Partizanskaya cave (the Mana river basin – two skulls in Zoological Institute collection), Kuzyakin (1950) and Bobrinskiy et al. (1965) reported one finding in Dodonova village, north of Krasnoyarsk. There is one young male from Angara river (Irkutsk district) deposited in the Mammal collection of the Zoological Institute, St. Petersburg. There is one locality in the Altai region: Kebezen village on the Biya river, 20 km from Teletskoye lake (Bobrinskiy et al. 1965); the place of its storing is unknown, nevertheless we suggest it belongs to the newly described subspecies (Fig. 1). *M. f. eniseensis* inhabits mountains of southern taiga. The largest part of the specimens was found in their hibernacula in caves.

**Myotis bucharenensis** Kuzyakin, 1950

**Type.** Adult female, No. 50002, Zoological Institute of Russian Academy of Sciences (St. Petersburg). Aiwadj, SW Tadzhikistan. August, 1915, collected by V.J. Lazdin.

**Diagnosis.** Coloration is of light, “desert” type. Back, membranes and ears are light pale-brown, abdomen is almost white. Tail is long (more than 100% of body length). Ears are not wide as they are in *M. f. longicaudatus*, and abruptly narrowed to their rounded tips, tragus is longer than half of the pinna length. Margin of plagiopatagium is attached to distal portion of metatarsus of the first toe. Skull is relatively long, not so broadened and has lesser sharp flexure in its frontal part (in profile) than in *M. f. longicaudatus* (Fig. 2); brain case is high, slightly inflated. Upper canines are relatively rounded, there are two deep grooves on their lingual sides and two expressed ones on the labial side of each upper canine (Fig. 3). The third upper premolar (P3) is greatly displaced from the tooth row. A metaloph is present on M1 and M2, but no protoconules.

Wallin (1969) considered the Bocharic bat to be a lighter-coloured form of *M. frater* and restricted it to *M. f. bucharenensis*. We consider *M. bucharenensis* to be a distinct species on the basis of its different body size and skull, and teeth construction details.
Distribution. Apart from the type locality, this form is known from the Samarkand vicinity only (Uzbekistan) (Fig. 1). *M. bucharensis* may probably be a speleobiont living in colonies. The single known colony of this species of ca. 500 individuals, consisting of pregnant and lactating females, was found in an artificial cave near Samarkand. Both localities are placed in large river valleys of foothill regions, where the climate is arid enough.

Comparison between examined forms

External characters. *M. bucharensis* greatly differs from others by pelage coloration: it is light, typically “desert”. The other longtailed mouse-eared bats are usually dark brown. *M. bucharensis* (as the largest representative) and *M. f. longicaudatus* (as the smallest one) are reliably distinct. *M. f. eniseensis* has the longest ears and the shortest tail.

The wing shape in all these forms is similar; *M. f. longicaudatus* differs from others by relatively short distal phalanges of the third and the fourth digits.

The terminal lobe is present in all the forms. Kuzyakin (1950) pointed out, that the calcar lobe of *M. f. longicaudatus* possesses a keel, but not that of *M. bucharensis*. In the type specimen of *M. bucharensis* a calcar lobe keel is absent indeed, but in 4 specimens from Samarkand it is well developed. The calcar lobe in *M. f. kaguyae*, deposited in Zoological Institute RAS, is well developed, too. In one specimen of *M. f. longicaudatus* it bears a more or less developed keel, while another one, from the Angara river (Krasnojarsk district), has it on its left foot only. Thus, the presence or absence of this structure is not a good character for this group; however, in all *M. f. eniseensis* specimens known to us, the keel was absent.

![Fig. 4. The disposition of samples of the examined taxa in the two canonical variables space.](image-url)
Taxonomy of the *Myotis frater* species group

In the subspecies of *M. frater* (excluding *M. f. eniseensis*) and in *M. bucharensis*, the interfemoral membrane has single hairs on the inside, and these hairs form small bunches only at the tail base. In *M. f. eniseensis*, the inside of the membrane carries bunches of hairs on two thirds of the tail length from its base.

**Skull.** The two types of skull profiles are characteristic of these bat species (Fig. 2). The first one is characterised by strongly abrupt nose-frontal crook and shorter rostral part (*M. f. frater*, *M. f. longicaudatus*, *M. f. kaguyae*); in the other type the rostrum is relatively long and rises smoothly (*M. bucharensis* and *M. f. eniseensis*) enough.

The skull shapes for all the forms were compared through stepwise discriminant functional analysis. First all the 19 cranial measurements were taken into account, and only 10 of them (the most significant ones) had been taken into the final analysis. The stepwise discriminant function analysis has revealed a high level of discrimination between the subspecies and 100% correct definition of all specimens (Fig. 4).

**Teeth.** No grooves can be found on back-labial sides of upper canines in *M. f. eniseensis*, but there is one in *M. f. frater* (deep in *M. f. kaguyae* and small in *M. f. longicaudatus*) and two well expressed grooves in *M. bucharensis*. All forms differ in general shape of the upper canines (see diagnosis and Fig. 3).
The third upper premolar, displaced outside the tooth row, when P2 is in contact with P4, is a characteristic feature of the *Myotis frater* group. Moreover, some specimens lack P3 at all. The fourth upper premolar (P4) lacks or bears a small cingular crisp. Several different opinions about protoconule presence on M1–M3 in the group exist at the same time. Yoshiyuki (1989) considered that protoconules are not characteristic for the *M. frater* group, while Imaizumi (1956) cited the presence of this structure in the species diagnosis for *M. f. kaguyae*. We succeeded in finding just little protoconules in two specimens of *M. f. kaguyae* and *M. f. longicaudatus* deposited in Zoological Institute RAS. Several individuals of *M. f. eniseensis* have almost reduced protoconules. *M. bucharensis* lacks them. Paraloph and metaloph on M1 and M2 are present in all forms. It is worth mentioning, that the metaloph on M1 and M2 is very low in *M. f. eniseensis* and can be indistinguishable for the effaced teeth.

**Baculum.** The baculum shape is common for the *Selysius* subgenus and is well distinguishable through its form (Strelkov 1989; Yoshiyuki 1989; see Fig. 5). In *M. f. longicaudatus* the baculum is of a maximum size, more massive and not markedly narrowed at its medial part ("waist") as in other subspecies. The smallest and the narrowest baculum is characteristic of *M. f. frater*, and in *M. f. eniseensis* it shows high similarity with that of *M. f. kaguyae*.

**Discussion**

The *Myotis frater* species group is not homogenous and includes several forms of subspecific rank. In connection with this fact the *Myotis frater* species group comprises two distinct species: *M. frater* Allen, 1928 (now including the following four subspecies: *M. f. frater*, *M. f. kaguyae*, *M. f. longicaudatus* and *M. f. eniseensis*) and *M. bucharensis* Kuzyakin, 1950.

The cluster diagram we present here, reflects our point of view on the relationship among the examined forms (Fig. 6).

The *Myotis frater* species group combines *Leuconoe* and *Selysius* traits and most probably takes up an intermediate position. Godawa-Stormark (1998) showed *Myotis frater* s.l. to have an intermediate (between *Selysius* and *Leuconoe*) type of dentition, besides *M. bechsteinii* and *M. ater*.

Imaizumi (1956) mentioned that the skull in *Myotis frater* had a “remarkably high braincase and short rostrum, breadth of braincase evidently more than half of the greatest length of skull as in the subgenus *Leuconoe***. At the same time he cites "external characters rather similar to those of the typical *Selysius*, especially to *Myotis siligorensis***. The presence of the two different types of skull profile in *M. f. kaguyae* was mentioned by Yoshiyuki (1989). Besides some other differences she supposed it to be possible to suggest two distinct subspecies for *M. f. kaguyae*.

Ognev (1928) supposed *M. f. longicaudatus* to be close to *Myotis davidi*, referred to *Leuconoe* by Ellerman & Morrison-Scott (1951). Findley (1972), Corbet (1978) and Koopman (1994) on the other hand, referred to it as *Myotis mystacinus*. The main evidences used to bring these forms closer to each other were small size and the displacement of P3 from the tooth row.

A. Borissenko (Zoological Museum of Moscow University) suggested to unite *M. frater*, *M. bucharensis* and *M. davidi* in a distinct subgenus (in litt.).
Taxonomy of the *Myotis frater* species group

![Image of a single linkage tree showing dissimilarities from matrix.](image)

**Fig. 6.** Single linkage tree showing dissimilarities from matrix.

**Acknowledgements**

We are grateful to Dr. Nancy Simmons and Dr. Robert Voss (AMNH), Dr. Alexander Botwin-kin (Irkutsk) and Dr. Mikhail Tiunov (Vladivostok) for loaning the necessary material. We thank Dr. Sergey Kruskop and Alex Borissenko (Zoological Museum of Moscow State University) for valuable discussion of the problem. This work was supported by grant from RFFI (Russian Fund for Basic Research).

**Zusammenfassung**

Vier Subspezies innerhalb der Gruppe *Myotis frater* s.l. sind gemeinhin bekannt. Nach unserer Untersuchung ist *M. bucharensis* als gültige Spezies zu betrachten. *M. f. longicaudatus* beinhaltet zwei geographisch isolierte und morphologisch unterschiedliche Formen: *M. f. longicaudatus* bewohnt den Fernen Osten (Typus-Region), *M. f. eniseensis* ssp. nov. die Krasnoyarsk-Region in Mittelsibirien.

**References**


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