

A new species of South-East Asian *Myotis* (Chiroptera: Vespertilionidae), with comments on Vietnamese ‘whiskered bats’

SERGEY V. KRUSKOP^{1,3} and ALEX V. BORISENKO²

¹Zoological Museum, Moscow State University, Bolshaya Nikitskaya, 6, 125009 Moscow, Russia

²Biodiversity Institute of Ontario, University of Guelph, Guelph, Ontario, Canada N1G 2W1

³Corresponding author: E-mail: kruskop@zmmu.msu.ru

A new *Myotis* species is described from Central Vietnam and adjacent area of Laos. The new species resembles smaller specimens of the widespread South Asian *Myotis muricola*, though differs from it and from other small mouse-eared bats by a set of cranial and external characters. Genetic analyses confirm that the new species is distinct from the other named forms of Asian *Myotis*. Comparison of sequence diversity in the DNA barcode region of the COI gene among East Asian members of *Myotis*, highlighted several taxonomic questions related to Asian ‘whiskered bats’, suggesting that common morphological diagnostic traits may be shared by genetically divergent species.

Key words: *Myotis*, new species, South-East Asia, Vietnam, taxonomy, DNA barcoding

INTRODUCTION

The increasing volume of focused ecological and taxonomic surveys of Chiroptera in Vietnam has enriched its bat species list by over 20% during the past decade, with the present tally estimated at over 110 species (Borissenko and Kruskop, 2003; Can *et al.*, 2008). This was a result of both new geographic records and descriptions of new species. Furthermore, recent biodiversity genomic approaches (e.g., Francis *et al.*, 2010) have shown cryptic divergence within traditionally recognized morphological species, suggesting the taxonomic diversity of Vietnamese bats to be substantially underestimated.

Myotis is the second largest genus within Mammalia, containing more than 100 extant species (Simmons, 2005). Not surprisingly, it remains one of the prominent taxonomic ‘hot spots’ both within Vietnam and beyond. While the taxonomic hierarchy within *Myotis* was completely revamped in recent molecular studies (Ruedi and Mayer, 2001; Stadelmann *et al.*, 2007), many questions remain unresolved concerning the alpha taxonomy of several species groups. In particular, the delineation of species often remains challenging, especially in tropical faunas. Recent descriptions of two new species from East Asia (Borisenko *et al.*, 2008; Tiunov *et al.*, 2011) reflect the fact that taxonomic

diversity within *Myotis* is still poorly known. This taxonomic impediment, reinforced by the growing number of collections and the limited curatorial attention they receive, calls for new taxonomic revisions and descriptions at both regional and global scales.

Within *Myotis*, the ‘*mystacinus*’ morphological group, colloquially referred to as ‘whiskered bats’, is one of the key taxonomic ‘stumbling blocks’. Traditionally, this group formed the bulk of the morphologically ‘primitive’ subgenus *Selysius* (Tate, 1941; Koopman, 1994), whose paraphyletic nature was later shown in a series of molecular studies, leading to its abolishment (Ruedi and Mayer, 2001; Hooper and Van Den Bussche, 2003; Stadelmann *et al.*, 2007). Despite these systematic findings, many small Old World *Myotis* with *mystacinus*-like appearance are hard to distinguish in the field (Dietz and von Helvesen, 2004; Kawai *et al.*, 2006). The lack of proper revision within this species group has resulted in the species epithet ‘*mystacinus*’ misapplied to specimens from mainland Southeast Asia (Bates *et al.*, 1999; Kuznetsov, 2006; Francis, 2008) even after the Palaearctic forms of *M. mystacinus* have been revised and split into several species, and the range of the nominotypical form was shown to be restricted to Europe (Benda and Tsytsulina 2000).

While processing a collection of Asian *Myotis* using a combined morphological and molecular approach (Francis *et al.*, 2010), we found several cases of supposed cryptic diversity that led to further taxonomic enquiry. A small collection of bats made by AVB as part of an ecological assessment in the Vu Quang Nature Reserve, Ha Tinh Province, Vietnam, contained several specimens of small mouse-eared bats, provisionally identified as '*M. siligorensis*' (Borissenko and Krusko, 2003; A. V. Borisenko, S. V. Krusko, and N. V. Ivanova, unpublished data). Further in-depth comparison with a larger series of South-East Asian *Myotis* demonstrated clear morphological differences of the Vu Quang specimens from *M. siligorensis* and related forms which were corroborated by deep genetic divergence in the DNA barcode region of the cytochrome oxidase subunit 1 (COI) gene. This combined evidence suggests that the Vu Quang series represents a new bat species; its description is provided herein.

MATERIALS AND METHODS

Specimen Collecting and Processing

Bats were captured in their flight paths and foraging areas with mist nets and flap traps (Kunz and Kurta, 1988; Borisenko, 1999; Borisenko and Krusko, 2003). All captures took place within the first three hours following sunset. Individuals intended for vouchers were euthanized with chloroform vapours, following recommended protocols (American Society of Mammalogists Animal Care and Use Committee, 1998).

Four external measurements (head and body, tail, ear and forearm length) were taken post-mortem with digital callipers. Specimens were fixed in 75% ethanol within 10 to 15 minutes after euthanasia. Subsequent processing of collection material resumed within several months following fixation. External measurements were taken with vernier or electronic callipers to the nearest 0.1 mm. Skulls of seven specimens were extracted and cleaned in a dermestarium. Cleaned skulls were measured under a dissecting microscope with electronic callipers to the nearest 0.01 mm. Tissue samples for DNA extraction were not collected on the day of capture and had to be taken at a later date from muscle of alcohol-preserved specimens.

Comparative Material

One hundred and twenty six bat specimens were used in quantitative morphological analysis, selected to represent different populations of *M. muricola* sensu lato, and also *M. ater*, *M. gomantongensis*, *M. montivagus*, *M. nipalensis* and *M. siligorensis* (including the paratypes of *M. s. alticraniatus* used in an earlier study — see Borisenko *et al.*, 2008). All specimens were adults of both sexes, preserved either as dry skin and skull vouchers or as fluid-preserved carcasses with extracted skulls. Seventy three specimens were included in molecular analysis. Additional specimens of *M. muricola* sensu lato, *M. phanluongi*, *M. annectans*, *M. sicarius* and *M. moupinensis* were used for qualitative comparison. A detailed list of

specimens studied is provided below. Acronyms of repositories of the processed collections are as follows: FMNH — Field Museum of Natural History, Chicago; GMNH — Geneva Museum of Natural History, Geneva; HNHM — Hungarian Natural History Museum, Budapest; ROM — Royal Ontario Museum, Toronto; SMF — Senckenberg Museum, Frankfurt am Main; ZMB — Zoological Museum of Berlin (Museum für Naturkunde); ZMMU — Zoological Museum of Moscow State University, Moscow; ZISP — Zoological Institute, Russian Academy of Sciences, St. Petersburg.

Myotis muricola: India: HNHM92.106.1. (♀); Nepal HNHM98.5.24. (♀), ZMMU S-164491 (♂), ZMMU S-164492 (♂); Myanmar: ZMB 3400 (♂, type of *M. lobipes*) Malaya: ROM MAM 38001, 38002, 38183, 38194 (♀ ♀), ROM MAM 38182, 40008, 40009, 40943 (♂ ♂), ZMB 4099; Java: ZMMU S-103262, 103263, 103265, 103269 (♀ ♀), ZMMU S-103257, 103264, 103266, 103268 (♂ ♂), ZMB 67004, 67005, 67006 (sex unknown); Sumatra: HNHM 2869/3, ZISP 84715, ZISP 84717, ZISP84718, ZISP84719 (♂ ♂); Borneo: ROM MAM 117947, ZMB 48336 (♀ ♀), HNHM2869/23.1, HNHM2869/23.2, ROM MAM 117943, 117944, ZMB 48335 (♂ ♂); Pulau Sumba: ZMB 54615, 92153, 92155 (♀ ♀), ZMB 92157 (♂), ZMB 92152 (sex unknown); North Vietnam: ZMB 54034 (sex unknown); Central Vietnam: ZMMU S-165048 (♀), ZMMU S-165055 (♂), ZMB 62613 (sex unknown); S. Vietnam, Lam Dong Prov.: ZMMU S-172611, 172615, 172620, 173410 (♀ ♀), ZMMU S-172619 (♂); South Vietnam, Tai Ninh Prov.: ZMMU S-172623, 172624, 172629, 172631 (♀ ♀), ZMMU S-172626, 172630 (♂ ♂); South Vietnam: ZMMU S-184680, 186603, 188173 (♀ ♀), ZMMU S-188181, ZISP 5930 (♂ ♂); China, Guangxi: ROM MAM 116134, 116423 (♀ ♀); *M. aff. muricola*: China, Guizhou: ROM MAM 117808, 117809 (♂ ♂); Central Vietnam: ROM MAM 111270 (♀); *M. ater*: South Vietnam: ZMMU S-172605, 172606, 186580, 186582, 188172 (♀ ♀), ZMMU S-172604, 172608, 186591, 188199 (♂ ♂); Laos: SMF 86175, 86176 (♀ ♀); Thailand: SMF 88664 (♀); The Moluccas: ZMB 2956 (sex unknown, cotype of *M. ater*), ZMB 3119 (♀, type of *M. amboinensis*); *M. montivagus*: Laos: ROM MAM 106526 (♀), ROM MAM 106525, SMF 94080 (♂ ♂); Central Vietnam: ZMMU S-164999 (♀); N. Vietnam: ZMMU S-186703, 186704 (♀ ♀), ZMMU S-186529 (♂); China: ROM MAM 116431, 116469 (♂ ♂); *M. nipalensis*: S. Turkmenistan: ZMMU S-104448, 104449 (♀ ♀), ZMMU S-29214 (♂), ZMMU S-29222 (sex unknown); Uzbekistan: ZMMU S-6819, 94702 (♀ ♀), ZMMU S-29225, 94703 (sex unknown); *M. gomantongensis*: Borneo, Sabah: ROM MAM 107812, 112102, SMF 83729, 83730, 83731 (♀ ♀), ROM MAM 107809, 107810 (♂ ♂); *M. siligorensis*: China: ROM MAM 116118, 116119, 117796, ZMB 76984 (♀ ♀); Vietnam: ZMMU S-167187, 175159, FMNH 32173, 32175, 32178 (♀ ♀); Thailand: SMF 88963, 88964, 88966, 88968, 88970, 88971 (♂ ♂); *Myotis annectans*: Laos: ROM MAM 106387, 106390, 106408 (♀ ♀); Sumatra: ROM MAM 86357 (♀), ROM MAM 86356 (♂); *M. sicarius*: Nepal: ZMMU S-164494 (♀), ZMMU S-164495 (♂); *M. phanluongi*: Central Vietnam: ZMMU S-175153, 175154, 173156 (♀ ♀), ZMMU S-175155 (♂); '*M. caliginosus*': Himalayas: ZMB 3118 (♀); '*M. blanfordi*': India, Sikkim: ZMB 4117 (♀), ZMB 4373 (sex unknown) — cotypes of *M. blanfordi*; '*M. moupinensis*': China, Sichuan: ZISP 5510-11 (♀), ZISP 5508, 5512 (♂ ♂); '*M. latirostris*': Taiwan: GNHM with no ID-number.

A total of 357 specimens representing 25 valid named forms of *Myotis* from East Asia were analyzed for patterns of genetic

divergence in the DNA barcode region of COI. Comparative sequence information was taken from data published in connection with earlier projects (Francis *et al.*, 2010; Kruskop *et al.*, 2012) and housed by the Barcode of Life Data Systems (BOLD; www.boldsystems.org). The complete set of molecular data used in this study can be reviewed as an online dataset at: http://www.boldsystems.org/index.php/Public_SearchTerms?query=DS-ABSKMA; DOI – [dx.doi.org/10.5883/DS-ABSKMA](https://doi.org/10.5883/DS-ABSKMA). A list of BOLD Process ID numbers is provided in the Appendix.

Morphometric Analyses

The following external measurements were taken from fluid-preserved carcasses or dry skins: forearm length, tibia length, foot length (including claws, measured to the distal extremity of the claws), length of the first digit (including claw), length of the metacarpal of the second digit, and lengths of the metacarpals and phalanges of the third, fourth and fifth digits. All wing measurements were taken on the right wing, unless unsuitable (e.g., damaged) or inaccessible for measuring. The following cranial measurements (abbreviations given in parentheses) were taken: condylobasal length (CBL), condylocanine length (CCL), occiput height (OH), mastoid width of skull at the level of the auditory bullae (MW), width of braincase (BCW), least interorbital width (IOW), rostral width at the level of the infra-orbital foramina (RW), rostral length from anteorbital foramina to the alveolus of the inner incisor (RL), C–M³ length (CM³), molariform row length (P⁴M³), length of the upper canine cingulum base (C), length of interval between cingula of upper canine and large premolar ('pseudodiastem', Pseud), width between the outer margins of the upper canines at the crown (CC), width between the outer margins of M³ at the crown (M³M³), width of M² (M²), lower jaw length from alveolus of i1 to the glenoid process (MdLg), lower jaw length from alveoli of i1 to the angular process (MdLa), crown length of maxillary tooth row (CM₃), crown length of maxillary molariform row (P₄M₃), lower jaw height to the tip of coronoid process (MdH).

To assess the pattern of variation of quantitative characters, Principal Component (PC) and Discriminant Function (DF) analyses were performed for cranial measurements, using the Discriminant Function and Principal Component Analysis and Classification modules of STATISTICA for Windows version 7.0 (StatSoft, Inc., 2004). Eighty six individuals were involved in analysis representing seven putative species; however samples of *M. gomotongensis* and *M. montivagus* were then excluded because their definitely larger size made too much influence on the first factor. DF analysis was used to calculate squared Mahalanobis distances between groups.

Molecular Analyses

Molecular analyses were performed by the staff of the Canadian Centre for DNA Barcoding (CCDB), University of Guelph, Canada. The standard DNA barcode region — 657 base pair 5' segment of the mitochondrial cytochrome oxidase subunit I (COI) gene — was sequenced bidirectionally using standard DNA barcoding protocols for mammals (Ivanova *et al.*, 2006, 2012; Clare *et al.*, 2007; Borisenko *et al.*, 2008). Whole genomic DNA from ethanol-preserved tissue was recovered using an automated DNA extraction method. PCR amplification for the standard DNA barcode region was done using M13-tailed primer cocktails C_VF1LFt1 and C_VR1LRt1. PCR products were sequenced using an ABI Prism BigDye Terminator ver.

3.1. Cycle Sequencing kit and analyzed on ABI 3730XL Genetic Analyzer. Sequences were assembled and manually edited in CodonCode Aligner 3.7.1 software (CodonCode Corporation) by CCDB sequencing technicians. For this study, DNA barcode sequences were obtained from the holotype of the new species (ZMMU S-165042).

Analysis of molecular COI data was performed using MEGA ver. 5 molecular genetic analysis software (Tamura *et al.*, 2011). A distance-based tree with 357 specimens was built with the Neighbour-Joining algorithm using the maximum composite likelihood model (Tamura *et al.* 2007) and pairwise deletion of missing data. The rate variation among sites was modeled with a gamma distribution (shape parameter = 1). Branch support was assessed by bootstrapping with 500 replicates.

RESULTS

Bivariate scatterplots of skull measurements (Fig. 1) suggest that *mystacinus*-like *Myotis* from Indochina fall into three major size groups. The largest specimens appear to represent *M. montivagus*. Specimens from North Vietnam agree in skull proportions with the type specimen from China (according to measurements provided by Benda, 2010). The remaining specimens, including one from Central Vietnam are even larger and may represent another taxon. Mid-sized bats are represented by *M. ater* and the extralimital *M. gomotongensis*. The smallest species are *M. muricola* s. lato and *M. nipalensis*. We were unable to measure *M. nipalensis* from the northern part of the Indian subcontinent; the specimens in our analysis originated from the Central Asian part of the species range (Benda and Tsytulina, 2000) and agree with the diagnosis given in the latter work. They also match the measurements provided for Indian individuals by Benda (2010). *M. siligorensis* is distinctly smaller than *M. muricola* in skull measurements. The series from Vu Quang occupies a size range intermediate between *M. siligorensis* and *M. muricola*, only slightly overlapping with the latter.

A bivariate scatterplot of the first two Principal Components provides the best separation (Fig. 2 and Table 1). The Vu Quang series is clearly separated from *M. muricola* and *M. nipalensis*. The combination of the second and fourth Principal Components (not shown) clearly separates *M. muricola* and *M. nipalensis* from each other and separates most *M. ater*, although with some overlap with *M. muricola*. Discriminant Function analysis shows significant difference between all the analysed species samples ($P < 0.001$), although the difference between three samples of *M. muricola* (from Vietnam, Java and Sumatra, and Malaya) is insignificant. The new species is distant from all other species

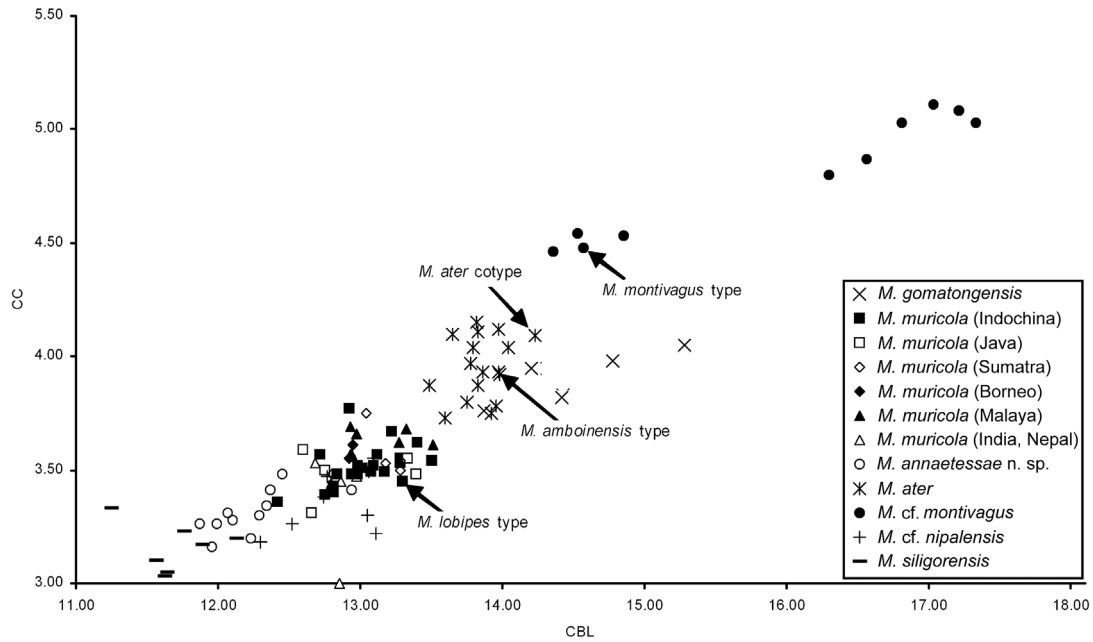


FIG. 1. Bivariate scatterplot for CBL versus CC measurements in 111 specimens representing Asian ‘whiskered’ *Myotis* species. Measurements of the *M. montivagus* type were taken from Benda (2010)

analysed; its mean squared Mahalanobis distances from other species exceeding intraspecific values by 3–6 times (Table 2).

All analysed species of the ‘*mystacinus*’ morphogroup possess a medium-sized (0.7–1.1 mm) saddle-shaped baculum with a relatively massive and elevated proximal base, widened medial portion, blunt tip, curved upper profile and well-defined

urethral groove. Two bacular morphotypes can be defined within this general pattern. In *Myotis ater* and *M. muricola* from Indonesia and Indochina, the highest point of the lateral projection is located near the mid-part of the penial bone, while its tip narrows abruptly and is curved towards the urethra (Fig. 3). By contrast, in the baculum of *M. montivagus*, *M. muricola* from Nepal and of the new species

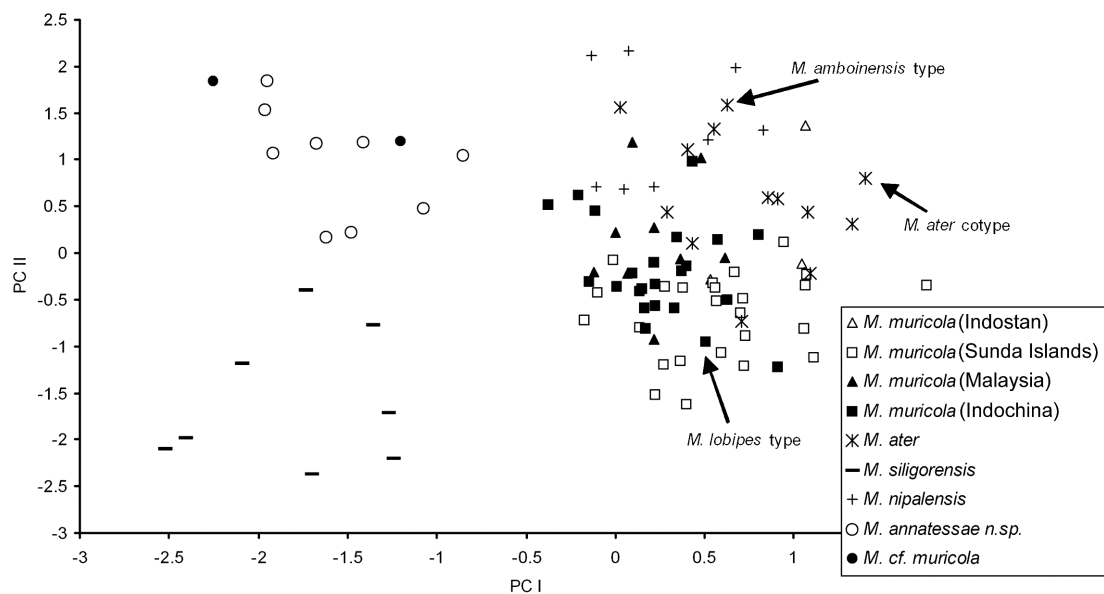


FIG. 2. Bivariate scatterplot for the 1st and 2nd Principal Components, calculated for 20 cranial and dental measurements of 100 specimens of small Asian mouse-eared bats. For factor loadings and eigenvalues, see Table 1

TABLE 1. Factor loadings and eigenvalues for the first four factors of the Principal Component analysis (see Materials and Methods for measurement explanations)

Measurement	Factor 1	Factor 2	Factor 3	Factor 4
CBL	0.814	0.328	-0.065	0.411
CCL	0.807	0.316	-0.056	0.448
OH	0.311	0.210	0.026	0.842
MW	0.632	0.459	-0.002	0.543
BCW	0.273	0.848	0.052	0.281
IOW	0.289	0.839	0.064	0.188
RW	0.421	0.215	-0.088	0.722
RL	0.823	0.235	-0.039	0.209
CM ³	0.891	0.233	-0.053	0.348
P ⁴ M ³	0.877	0.263	0.131	0.336
C	0.863	0.206	0.178	0.225
PD	-0.032	-0.076	-0.992	0.026
CC	0.646	0.273	0.032	0.620
M ³ M ³	0.494	0.224	0.020	0.658
WM ²	0.842	0.206	0.034	0.397
MDLG	0.858	0.236	-0.048	0.424
MDLA	0.823	0.234	-0.097	0.475
CM ₃	0.908	0.241	-0.013	0.305
P ₄ M ₃	0.870	0.300	0.111	0.289
MDH	0.839	0.106	0.033	0.357
Eigenvalue	14.84	1.21	1.12	0.74
% total variance	74.18	6.03	5.61	3.72
Cumulative eigenvalue	14.84	16.04	17.16	17.91
Cumulative % of variance	74.18	80.21	85.82	89.53

from Vu Quang, the highest point is shifted towards the posterior half or third, while its dorsal profile is less concave and the distal tip is wider, more blunt and straight.

A NJ analysis of the DNA barcode regions of COI (Fig. 4) shows that the new species belongs to a distinct haplogroup cluster separated from *M. muricola*, *M. siligorensis* and *M. mystacinus* by a pairwise distance of at least 15%. It should be noted that the analyzed representatives of *M. muricola* are geographically remote from the type locality in the Himalayas (Corbet and Hill, 1992), and no genetic data are available from Nepal.

A combination of qualitative craniological traits, morphometric and genetic data suggests that the series of *mystacinus*-like bats from Vu Quang represents a separate unnamed species, whose description is provided herein.

Myotis annatessae sp. nov.

Holotype

ZMMU S-165042 (alcohol-preserved, skull extracted), adult male; Song Con river valley, Saola Basecamp, Vu Quang, Ha Tinh Province, Vietnam. 30.07.1997; coll. A. V. Borisenko.

TABLE 2. Squared Mahalanobis distances from group centroids for nine specimens of *M. annatessae* sp. nov. Groups 'muricola1', 'muricola2' and 'muricola3' correspond to samples of *M. muricola* from Vietnam, Sumatra and Java, and Malaya, respectively

ZMMU Catalog No.	Groups						
	muricola1	muricola2	muricola3	siligorensis	nipalensis	ater	sp. nov.
S-165042	102.07	125.19	137.41	84.17	138.33	185.06	20.04
S-164987	88.24	102.45	119.97	74.37	113.33	187.23	10.66
S-164989	98.08	122.09	126.90	62.17	151.03	199.53	24.73
S-165044	55.82	68.50	80.98	79.35	77.86	143.46	11.58
S-164988	91.59	113.47	120.77	113.12	123.32	187.94	20.81
S-165046	65.12	79.48	99.51	61.83	117.16	166.07	9.16
S-165047	65.26	89.22	97.35	83.67	106.27	145.58	14.31
S-164986	88.01	103.52	122.40	59.01	139.14	178.11	16.77
S-165043	63.98	90.61	98.47	99.94	101.55	131.11	22.90

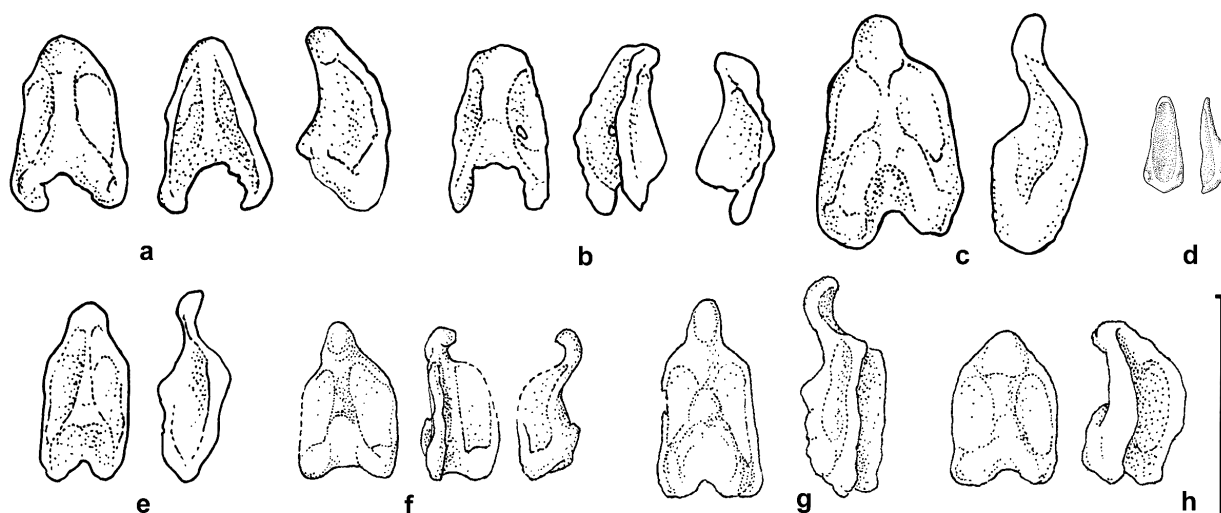


FIG. 3. Camera lucida traces of penial bones (bacula) in five smaller species of the Asiatic *Myotis*: a, b — *M. annatessae* sp. nov., Vietnam, ZMMU S-164989 (dorsal, ventral, right lateral views), ZMMU S-165043 (dorsal, ventro-lateral, right lateral views); c — *M. ater*, Vietnam, ZMMU S-172604 (dorsal, right lateral views); d — *M. siligorensis*, Vietnam, ZMMU S-167188 (ventral, left lateral views); e, f, g — *M. muricola*, Vietnam, ZMMU S-172616 (dorsal, right lateral views), ZMMU S-173413 (dorsal, ventro-lateral, left lateral views), ZMMU S-172626 (dorsal, right lateral views); h — *M. muricola*, Nepal, ZMMU S-164491 (dorsal, right ventro-lateral views)

Paratypes

Four adult females, ZMMU S-164986, 164988, 165046, 165047, four adult males S-164987, 164989, 165043, 165044 (alcohol-preserved, skulls extracted), 30.07–27.08.1997, same locality and collector.

Referred material

Two adult females, ZMMU S-165051–165052 (alcohol-preserved), same locality as type; one adult female, ROM MAM 106476, Nam Pan, N. of Lac 20, Khammouan Province, Laos, 20.04.1996; coll. C. M. Francis.

Type locality

Song Con river valley, Vu Quang, Ha Tinh Province, Vietnam.

Diagnosis

Small bat, similar in external, cranial and dental qualitative characters to *M. muricola* and to *Myotis mystacinus* sensu lato. Differs from *M. muricola* and *M. nipalensis* by smaller overall size, cranial dimensions and greatly reduced upper and lower canines, similar to those of *M. siligorensis*. Differs from *M. siligorensis* by a less concave frontal profile of the skull and myotodont lower molars. Differs from *M. muricola* by longer thumb and proportionally larger foot. Baculum is saddle-shaped but in details distinct from that of all the Indochinese *mystacinus*-like *Myotis* and bats of *M. siligorensis* lineage (Fig. 3).

DNA barcode of the holotype

GenBank accession JF443982, BOLD process ID ABBM488-07. DNA barcode sequence divergence from nearest neighbour is ca. 6%.

Measurements of the holotype (in mm)

External measurements: head & body 38, tail 37, forearm 34.3, hind foot 6.2, tibia 14.5, thumb (without claw) 5.3, ear pinna 13.2, wing span 230. Skull measurements: CBL 12.37, CCL 11.53, OH 5.22, MW 6.98, BCW 6.78, IOW 3.42, RW 3.52, RL 2.70, CM3 4.80, P4M3 3.52, C 0.62, Pseud 0.61, CC 3.41, M3M3 5.24, M2 1.25, MdLg 9.35, MdLa 9.57, cm3 5.09, p4m3 3.72, MdH 2.38.

Etymology

The species epithet is coined in honour of AVB's daughter, Anna Tess.

Description

Small-sized *Myotis* (FA ca. 32.6–35.3 mm, BM ca. 2.9–4.3 g.) similar in appearance to *M. muricola* or *M. mystacinus*. Tail shorter than head and body by about 5 mm. Fur not particularly thick, hairs relatively short (ca. 4–6 mm) extending by 4–5 mm onto the tail membrane. Pelage coloration greyish-brown on back and paler on belly. Individual hairs on back are blackish at bases gradually turning brown towards the tips; ventral hairs more contrastingly tricoloured, with blackish bases, brown

midportion and silvery-whitish tips. Genital area sparsely covered with white hairs. Hairless parts of skin mid-brown. Muzzle also covered by sparse

hairs almost up to the nostrils. Ears narrow, moderately long, reaching to the tip of muzzle if laid forward, bluntly pointed at tips, with very weak posterior emargination. Tragus bluntly pointed, relatively short, not reaching half of ear conch in height. Wing moderately long, with third metacarpal definitely longer than forth and fifth. Thumb proportionally long, with long and sharply pointed claw. Hind foot measured without claws about 42% of tibia length. Calcar lobe poorly developed. Wing membrane attaches to the base of the outer finger. Penis is relatively small, but not thin, slightly bulbously widened in distal half.

Skull small (average CCL 11.60 ± 0.24 mm; mean CM^3 4.79 ± 0.11 mm). In general appearance, the skull is intermediate between that of *M. muricola* and *M. siligorensis*: lightly built, with low and narrow rostrum (though more massive than in *M. siligorensis*), somewhat bulbous braincase and definite, but not deep concavity on the frontal profile (Fig. 5). In lateral view, highest part of skull is at the level of the supraoccipital bone. Sagittal and occipital crests absent, lambdoid crests poorly developed but visible. Zygomatic arch thin, without any vertical lobes. Anteorbital opening is situated over the posterior root of P^4 or over the gap between it and the first root of M^1 ; maxillary channel moderately short. Posterior palatal emargination is rectangular in shape. Basicranial pits are well-developed. Lower jaw with almost vertical anterior edge of coronoid process; angular process definitely longer than articular, its distal end somewhat curved upward.

Teeth are relatively gracile. Canines (especially lower) are small, only slightly exceeding corresponding posterior premolars in height. Upper canines thin, almost round in occlusal view, with shallow but definite outer and inner posterior grooves. Outer upper incisors are about 2/3 of inner incisors in crown area and slightly smaller in height. Inner incisor clearly bicuspidate; outer incisor with a definite supplementary cusp on its lingual side. Inner lower incisors are with rudimentary fourth cusps; middle and outer lower incisors definitely four-cusped. Small upper and lower premolars positioned within tooth rows. Cingulum of the large upper premolar with a well pronounced anterior cusp. Upper molars with only traces of hypocones and paraconules, with closed trigon basins. Lower molars of myotodont type, with well developed hypoconulid; talonids on M_{1-2} slightly larger than corresponding trigonids.

Baculum small, ca. 0.7 mm in length, saddle-shaped, with deep basal emargination and highest

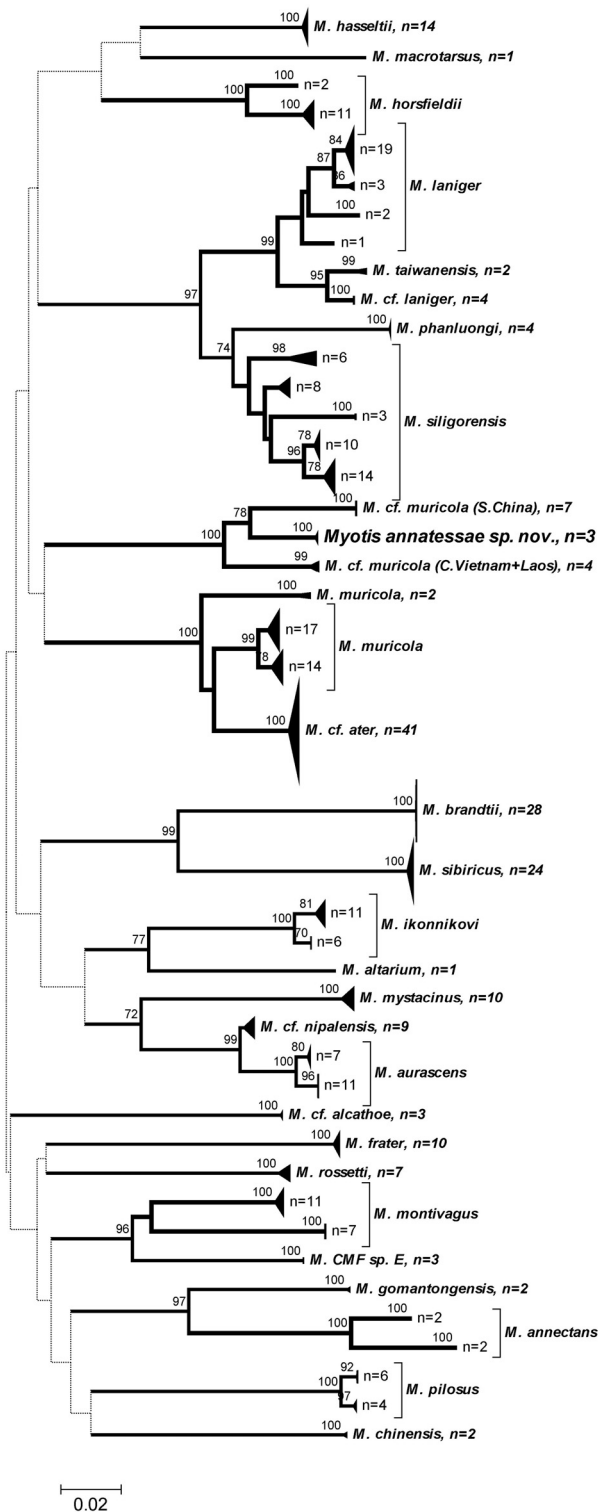


FIG. 4. Neighbour-joining tree of COI sequences of 25 species of Eurasian *Myotis* included in comparative molecular analysis (see Appendix for list of sequences used). Only bootstrap supports over 70% are shown

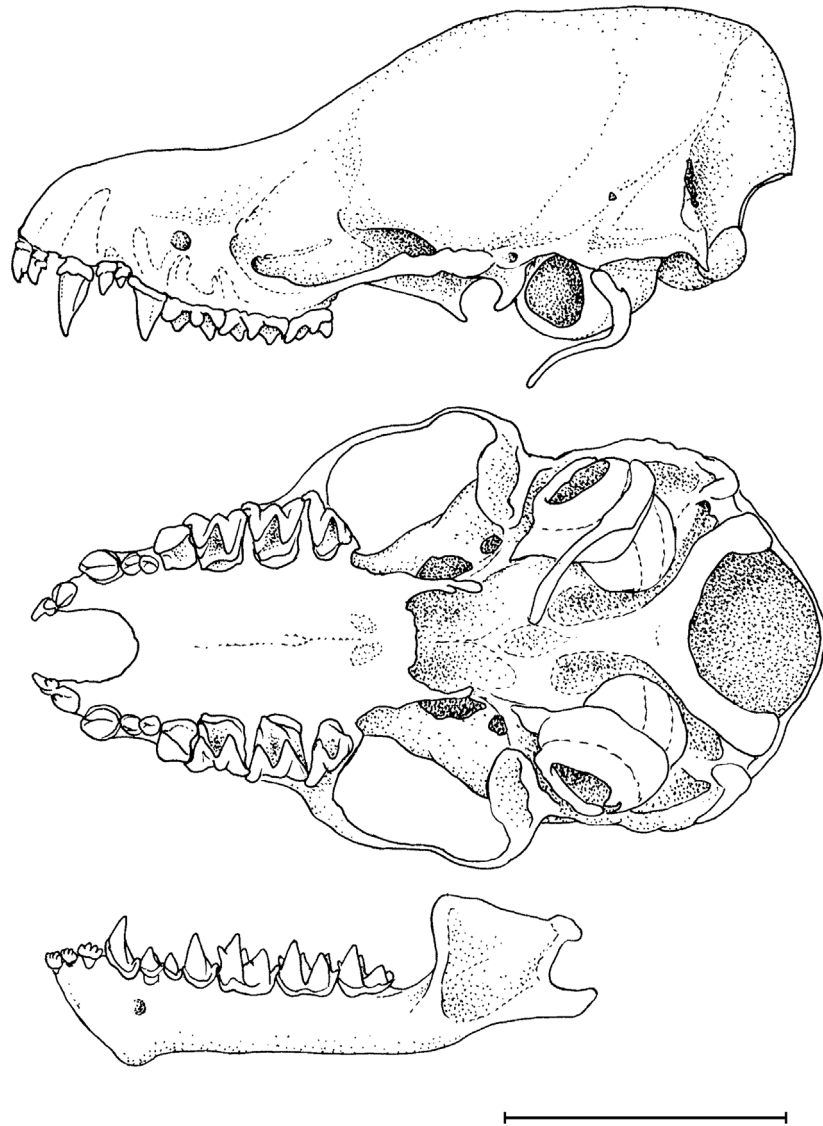


FIG. 5. Camera lucida tracings of the skull of *M. annatessae* sp. nov. (paratype ZMMU S-165043). Scale bar = 5 mm

point of the lateral projection just in front of it, approximately in the basal third (Fig. 3a, 3b). Urethral groove is deep and wide. Distal end of baculum blunt, without any abrupt constrictions.

Comparison to other species

The new species mostly resembles *M. muricola* s. lato in general appearance. It differs in smaller average size (both in external and cranial measurements) and weaker dentition with particularly small upper canines. The thumb and its claw is longer than in Indochinese and Malayan *M. muricola*; thumb measured without claw about 15% of forearm length (13.7–16.9 vs. 9.2–12.3% in *M. muricola*). The calcar lobe is less developed than in *M. muricola*. The notch on the posterior edge of the ear conch

is noticeably better developed in *M. muricola*. Penis is somewhat smaller and less bulbous than in Indochinese *M. muricola* and *M. ater*, but definitely thicker than in *M. mystacinus* s. lato. Indochinese specimens of *M. muricola* also have, on average, a proportionally shorter hind foot (about 38% of tibia length).

From *M. ater*, the new species also clearly differs in smaller size and lighter coloration. From *M. nipalensis*, it differs in a smaller upper canine and proportionally higher braincase: the average OH/MW ratio is 0.75 in *M. annatessae*, and 0.69 in *M. nipalensis*. From *M. siligorensis* and its allies the new *Myotis* differs by distinctively myotodont lower molars, larger canines (which exceed the corresponding large premolars in height), rectangular (not U

or W shaped) posterior edge of palate and a more robust rostrum.

The new species also differs from other morphologically similar *Myotis* in baculum shape. In the *M. siligorensis* complex, the baculum is minute and peg-like, often lacking the urethral groove. In Indochinese *M. muricola* and *M. ater* it is clearly different, with a constricted distal end. Amongst all the specimens analyzed, the baculum of *M. annatessae* bears closest resemblance to that of the Nepalese *M. muricola*, but the latter is more robust, more curved upward and has very shallow basal concavity (Fig. 3, h).

From *M. laniger* and small individuals of *M. horsfieldii*, the new species is easily distinguishable by a smaller hind foot (about half of tibia length in both species and definitely shorter in *M. annatessae*), by the place of the wing membrane attachment (above the base of the outer toe in both *M. laniger* and *M. horsfieldii*) and by shorter canines; from *M. rosseti* — by larger foot, larger overall size, absence of the adhesive pads on thumbs and both small middle upper premolars well developed. According to published data (Allen, 1938; Smith and Xie, 2008), *M. davidii* — another East Asian mouse-eared bat of similar size — has a larger hind foot and posterior upper small premolars displaced inward from the tooth rows.

Several other named forms of small-sized *Myotis* have been described from adjacent parts of mainland South-East Asia and were traditionally treated as subspecies of *M. muricola* (Simmons, 2005). *Myotis lobipes* from western Burma has long been regarded as a full synonym of *M. muricola* s. str. (Tate, 1941). Its type specimen resembles *M. muricola* specimens from Indochina in size and qualitative features.

Myotis moupinensis from China (not included into our analysis) is also usually treated as a partial synonym of *M. muricola* (Tate, 1941; Simmons, 2005). Its average smaller size (Allen, 1938) gives it superficial resemblance to *M. annatessae*. However, six alcohol-preserved specimens in ZISP, labelled as *M. moupinensis* and collected from within the known distributional range of this form, possess nyctalodont lower molars and other morphological traits in common with the Taiwanese *M. latirostris*. Thus they are more likely to be affiliated with this distinct species (*M. Ruedi*, personal communication). The same is probably true for *M. blanfordi* and *M. caliginosus*. Specimens of these forms (including types of *M. blanfordi*) processed in the Berlin Zoological Museum match *M. latirostris* in cranial shape and dentition. This entire species complex, while

similar in size to *M. annatessae*, differs markedly in having a lower braincase, shallower frontal profile, proportionally larger canines, and nyctalodont lower molars.

Finally, available skull measurements of the form *niasensis*, described from Nias Island as “a small form of *Myotis muricola*” (Lyon, 1916: 442), resemble those of the new species, but *niasensis* has shorter forearm and ear lengths (31.2–31.5 and 9.8–10.2 vs. 32.6–35.3 and 11.6–13.8, respectively). Tate, who apparently saw the type of *niasensis*, reports that it has a low brain case, in contrast to the proportionally high brain case in *M. annatessae*.

Genetic analysis

As mentioned earlier, neighbour-joining analysis of COI sequences (Fig. 4) corroborates the observed morphological distinctiveness of *M. annatessae* from both *M. muricola* and *M. siligorensis* complexes, as well as from the extralimital *M. mystacinus* and allied species. Available genetic data are insufficient to infer phylogenetic relationships between the new species and other *Myotis*, but its deep genetic divergence from the most morphologically similar representatives of this genus is clear. Closely related lineages, labelled on the tree as ‘*Myotis* cf. *muricola*’, most probably represent undescribed forms. However their divergence from *M. annatessae* also corresponds to specific level.

Comments on natural history

All Vu Quang specimens in the type series were captured over the Song Con River. Bats were observed foraging about 1–7 m above the water surface, over ripples as well as over backwaters. In the latter case *M. annatessae* were observed together with *M. horsfieldii*, although the latter was foraging immediately above the water surface; thus two species partitioned the foraging space by altitude. Echolocation calls recorded with a QMC Mini heterodyning ultrasound detector were FM, low intensity, with frequency ranging from 45–50 kHz. All specimens captured in July–August were reproductively inactive.

Distribution

We captured this species only in the type locality. The species is also known from Khammouane Province in Central Laos (ROM MAM 106476). The Laotian record was made approximately 40 km from the type locality. Morphologically and genetically similar specimens, though segregated by a relatively high genetic distance, were

collected in Ngoc Ling, Central Vietnam (ROM MAM 111270) and in Guizhou Province, China (ROM MAM 117808, 117809). Collecting localities were confined to large rivers in mountain foothills at elevations from 200 to ca. 1,300 m a.s.l.

DISCUSSION

At least three mouse-eared bat species occurring in Indochina have been assigned to the ‘*mystacinus*’ morphogroup: *M. muricola*, *M. ater* and *M. montivagus* (Corbet and Hill, 1992; Francis, 2008). Another species listed in recent Vietnamese checklists is *M. nipalensis* (Huynh *et al.*, 1994; Bates *et al.*, 1999; Can *et al.* 2008), commonly mentioned under the name *M. mystacinus* (e.g., Bates *et al.*, 1999, but see Smith and Xie, 2008). We did not examine any specimens mentioned in the above publications. *Myotis siligorensis* was also treated as a ‘whiskered bat’ (Bates and Harrison, 1997; Bates *et al.*, 1999), despite the fact that it possess distinctive morphological characteristics (Borisenko *et al.*, 2008; Tiunov *et al.*, 2011).

Myotis muricola in its traditional composition (e.g., sensu Corbet and Hill, 1992) is the most common and widespread *mystacinus*-like *Myotis* in tropical Asia; however, later studies argued that it represents a complex of distinct forms (Simmons, 2005). Several of those were recently raised to species rank. *Myotis browni* from the Philippines was shown to be deeply diverged, based on genetic data (Ruedi and Mayer, 2001; Zhang *et al.*, 2009), while the Taiwanese *M. latirostris* was putatively transferred to a separate genus (Lack *et al.*, 2010). As mentioned above, *M. blanfordi* has marked morphological similarities with *M. latirostris*; it should thus likely be excluded from *Myotis* as well. Based on morphometric material, Benda (2010) argued for the specific distinctiveness of *M. caliginosus* from northwest India. Available information on the forms *niasensis* and *moupinensis* (see ‘Comparison to other species’ above) suggests that they are also specifically distinct. A recent large-scale biodiversity genomic assessment of Southeast Asian Chiroptera (Francis *et al.*, 2010) found specimens referred to ‘*M. muricola*’ to be composed of a number of genetically divergent lineages, some of which are not nearest neighbours (see also Fig. 4).

The description of *M. annatessae* brings closure on one distinctive outlier; however, it also emphasizes the need for a thorough taxonomic reassessment of the remaining forms in this species

complex. Most collection-based information about *M. muricola* comes from parts of Indochina and the Sunda Islands — areas very remote from the type locality in Nepal.

Unfortunately, we have no molecular data for the Nepalese *Myotis* to compare the levels of morphological and genetic divergence. Our morphological analysis found no significant difference between *M. muricola* from the Great Sunda Islands, Malaya and mainland South-East Asia. By contrast, the few specimens available from Nepal have notable differences in craniometrics, thumb proportions, penial and bacular shapes. Benda (2010) obtained similar results; however, he also had very few Nepalese specimens available. This questions the validity of applying the name ‘*muricola*’ to Indochinese specimens and also raises the question of the appropriate scientific name that should be used for them if they prove to be specifically distinct. Based on our review of available type material, a plausible name to denote Indochinese and Indonesian specimens of ‘*Myotis muricola*’ would be *lobipes* Peters, 1867, described from Burma (Corbet and Hill, 1992).

Coincidentally, there is no clarity on the applicability of the name *Myotis ater* to bats from mainland Southeast Asia (C. M. Francis, personal communication), although examination of the cotypes of *M. ater* and type of *M. amboinensis* housed at ZMB did not provide a morphological basis for separating them from Asian mainland specimens identified as ‘*M. ater*’.

Despite the continuing reappraisal and refinement of phylogenetic affinities within *Myotis* based on molecular data (e.g., Ruedi and Mayer, 2001; Hofer and Van Den Bussche, 2003; Stadelmann *et al.*, 2007), there is a clear need for more baseline studies aimed at resolving species-level taxonomy. Many cases of ‘cryptic’ alpha-taxonomic diversity were highlighted in a recent study of the genetic divergence patterns in the DNA barcode region of COI among Southeast Asian bats (Francis *et al.*, 2010). This study shows good congruence between differences observed in subtle morphological characteristics and those seen in COI and further underscores the utility of a standardized single-gene approach as a tool for first-pass taxonomic assessment of taxonomically complex groups, such as *Myotis*. Particular attention should be paid to cross-referencing species identifications for specimens stored in different collections and curated by different experts and, ultimately, checking them against available type material.

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APPENDIX

List of the BOLD Process ID numbers for DNA barcode (COI) sequences used in the analysis. Source data can be reviewed and analyzed as an online dataset at: http://www.boldsystems.org/index.php/Public_SearchTerms?query=DS-ABSKMA; DOI — [dx.doi.org/10.5883/DS-ABSKMA](https://doi.org/10.5883/DS-ABSKMA)

Myotis altarium — ABCMA832-07.

Myotis annectans — ABBM148-05, ABBM138-05, BM134-03, BM205-03.

Myotis ater — ABBSI369-11, ABBSI368-11, ABBSI409-11, BM635-04, ABBSI408-11.

Myotis cf. *ater* — ABBSI237-10, ABBSI229-10, ABBSI250-10, ABBSI230-10, ABBSI239-10, ABBSI197-10, ABBSI193-10.

Myotis aurascens — SKBPA166-07, SKBPA164-07, SKBPA165-07, SKBPA226-07, SKBPA230-07, SKBPA606-11, SKBPA227-07, SKBPA231-07, SKBPA225-07, SKBPA617-11, SKBPA616-11, SKBPA618-11, SKBPA154-07, SKBPA609-11, SKBPA619-11, SKBPA620-11, ABCMA291-06, SKBPA607-11, SKBPA608-11, ABCMA292-06, ABCMA293-06.

Myotis cf. *aurascens* — SKBPA632-11, SKBPA635-11, SKBPA636-11, SKBPA634-11, SKBPA644-11.

Myotis brandtii — SKBPA133-07, SKBPA564-08, SKBPA134-07, SKBPA135-07, SKBPA563-08, SKBPA136-07, SKBPA295-07, SKBPA209-07, SKBPA208-07, SKBPA207-07, SKBPA273-07, SKBPA277-07, SKBPA097-07, SKBPA278-07, SKBPA291-07, SKBPA139-07, SKBPA283-07, SKBPA275-07, SKBPA287-07, SKBPA137-07, SKBPA352-07, SKBPA138-07, SKBPA654-11, SKBPA141-07, SKBPA146-07, SKBPA150-07, SKBPA140-07, SKBPA143-07, SKBPA142-07, SKBPA182-07, SKBPA548-08, SKBPA651-11, SKBPA652-11, SKBPA653-11, SKBPA147-07, SKBPA281-07, SKBPA206-07, SKBPA280-07, SKBPA294-07, SKBPA274-07, SKBPA293-07, SKBPA292-07, SKBPA132-07, SKBPA131-07, SKBPA129-07, SKBPA130-07, SKBPA148-07, SKBPA128-07, SKBPA167-07, SKBPA296-07, SKBPA205-07.

Myotis cf. *alcatheae* — SKBPA590-11, SKBPA591-11.

Myotis chinensis — ABBM469-05, BM358-03.

Myotis frater — SKBPA482-08, SKBPA480-08, SKBPA490-08, SKBPA567-08, SKBPA483-08, SKBPA210-07, SKBPA489-08, SKBPA481-08, SKBPA211-07, SKBPA568-08.

Myotis gomantongensis — ABBM392-05, ABBM393-05.

Myotis hasseltii — BM556-04, ABRVN430-06, ABRVN424-06, ABRVN423-06, ABRVN429-06, ABRVN419-06, ABRVN420-06, ABRVN427-06, ABRVN428-06, BM560-04, ABRVN426-06, ABRVN421-06, ABRVN422-06, ABRVN425-06.

Myotis horsfieldii — ABRLA057-06, SKMZM976-10, ABCMA537-06, ABBM094-05, ABBSI168-09, ABBSI173-09, BM173-03, BM047-03, ABBM078-05, BM115-03, ABBM179-05, ABRVN261-06, BM112-03.

Myotis ikonnikovi — SKBPA655-11, ABCMA198-06, ABCMA197-06, SKBPA145-07, ABCMA199-06, SKBPA545-08, ABCMA190-06, ABCMA176-06, SKBPA549-08, SKBPA581-10, SKBPA582-10, SKBPA099-07, SKBPA238-07, SKBPA580-10, SKBPA101-07, SKBPA102-07, SKBPA103-07.

Myotis laniger — SKMZM955-10, SKMZM957-10, ABRVN705-06, SKMZM956-10.

Myotis cf. *laniger* — ABRVN143-06, BM514-04, BM118-03, ABRVN136-06, BM231-03, ABRLA042-06, BM387-04, ABCMA013-06, BM215-03, ABRVN704-06, ABRVN703-06, ABCMA394-06, BM527-04, ABCMA368-06, ABCMA395-06, ABRVN142-06, ABRVN479-06, ABRVN134-06, ABRVN466-06, ABCMA012-06, ABCMA367-06, BM202-03, ABRVN137-06, BM400-04, ABCMA062-06.

APPENDIX. Continued

Myotis macrotarsus — BM116-03.

Myotis montivagus — ABBM282-05, ABBM262-05, ABCMA531-06, ABCMA519-06, ABCMA532-06, BM235-03, ABCMA487-06, ABCMA549-06, ABCMA459-06, SKMZM954-10, BM207-03, BM579-04, ABBSI288-11, ABBSI291-11, ABBSI287-11, ABBSI290-11, ABBSI289-11, ABBSI292-11.

Myotis CMF sp. E — BM197-03, BM201-03, BM114-03.

Myotis muricola — BM582-04, ABBSI393-11, ABBSI392-11, ABBSI156-09, ABBSI231-10, ABBSI354-11, ABBSI232-10, ABBSI391-11, ABBSI201-10, SKBPA503-08, ABBSI148-09, ABBSI227-10, ABBSI208-10, ABBSI214-10, ABBSI162-09, ABBSI353-11, ABBSI352-11, ABBSI377-11, ABBSI181-09, ABBSI233-10, ABBSI243-10, ABRVN309-06, ABBSI351-11, ABBSI242-10, ABBSI238-10, ABBSI370-11.

Myotis cf. *muricola* — BM601-04, ABBM120-05, ABBSI199-10, SKMZM989-10, ABBM488-07, ABRVN438-06, ABBSI198-10, BM545-04, BM613-04, ABBM076-05, BM361-04, ABRVN307-06, BM253-03, BM016-03, BM255-03, ABCMA511-06, ABBM129-05, ABRVN467-06, ABBSI196-10, ABCMA640-07, ABRVN198-06, ABRVN234-06, ABRLA145-06, ABRLA147-06, SKBPA070-06, BM535-04, BM214-03, BM212-03, BM225-03, ABRVN396-06, ABCMA089-06, BM117-03, ABRVN390-06, BM113-03, BM206-03, ABBM142-05, BM181-03, ABBM283-05, ABRVN306-06, ABBM082-05, BM213-03, ABRVN259-06, ABRVN308-06, BM060-03.

Myotis mystacinus — ABCMA801-07, SKBPA159-07, ABCMA833-07, SKBPA592-11, SKBPA160-07, SKBPA161-07, ABCMA760-07, ABCMA834-07, ABCMA870-07, SKBPA232-07, SKBPA085-07, ABCMA798-07, SKBPA163-07, SKBPA190-07, SKBPA151-07, SKBPA125-07, SKBPA233-07.

Myotis nipalensis — SKBPA628-11.

Myotis phanluongi — BM625-04, SKBPA507-08, SKBPA032-06, SKBPA020-06.

Myotis pilosus — BM220-03, BM038-03, ABCMA022-06, ABCMA014-06, ABCMA060-06, ABRLA055-06, BM236-03, ABBM406-05, SKBPA418-08, ABRLA054-06.

Myotis rosseti — ABBSI257-10, ABRVN341-06, ABBSI394-11, ABBSI395-11, BM544-04, ABRVN305-06, ABBSI246-10.

Myotis siligorensis — BM221-03, ABCMA631-07, ABCMA630-07, BM229-03, SKBPA021-06, ABRLA031-06, ABRLA032-06, SKBPA026-06, BM079-03, BM218-03, ABCMA869-07, ABRLA093-06, ABRVN674-06, ABRLA080-06, ABRLA033-06, ABBM250-05, ABRLA079-06, ABCMA731-07, ABRVN135-06, ABRLA105-06, ABBM324-05, BM232-03, BM051-03, ABBSI294-11, ABBSI293-11, ABCMA596-07, ABBM259-05, ABCMA077-06, ABCMA061-06, ABCMA050-06, ABRVN138-06, ABRVN153-06, SKBPA029-06, ABRVN155-06, ABCMA835-07, BM111-03, ABRVN673-06, ABRVN662-06, ABRVN663-06, ABBM274-05, ABRVN672-06.

Myotis taiwanensis — ABBM005-05, ABBM003-05.