



A new genus of vespertilionid bat: the end of a long journey for Joffre's Pipistrelle (Chiroptera: Vespertilionidae)

Tamás Görföls,[#] Sergei V. Kruskop,[#] Vuong Tan Tu,^o Péter Estók,^o Nguyen Truong Son,^o AND Gábor Csorba^{*,o}

Department of Zoology, Hungarian Natural History Museum, Baross utca 13, H-1088 Budapest, Hungary (TG, GC)

Zoological Museum, Moscow State University, Bolshaya Nikitskaya 2, 125009 Moscow, Russia (SVK)

Institute of Ecology and Biological Resources, Vietnam Academy of Science and Technology, N 18, Hoang Quoc Viet Road, Cau Giay District, 10072 Hanoi, Vietnam (VTT, NTS)

Graduate University of Science and Technology, Vietnam Academy of Science and Technology, N 18, Hoang Quoc Viet Road, Cau Giay District, 10072 Hanoi, Vietnam (VTT, NTS)

Department of Zoology, Eszterházy Károly University, Eszterházy tér 1, H-3300 Eger, Hungary (PE)

* Correspondent: csorba.gabor@nhmus.hu

[#]Shared first authors.

Knowledge as to the taxonomic status of enigmatic bat species often is hindered by limited availability of specimens. This is particularly true for aerial-hawking bats that are difficult to catch. One such species, “*Hypsugo joffrei*”, was originally described in *Nyctalus* due to its long and slender wings, but subsequently transferred to *Pipistrellus*, and most recently to *Hypsugo*, on the basis of morphology. Analysis of newly available material, which more than doubles the known specimens of this taxon, demonstrates that it is morphologically and genetically distinct from all other bat genera. We accordingly describe it as belonging to a new, monotypic genus. We provide a detailed description of its external and craniodental traits, measurements, and assessment of genetic relationships, including barcode sequences to facilitate its rapid identification in future. The new genus belongs to a group that includes the recently described *Cassistrellus*, as well as *Tylonycteris*, and its closest relative, *Philetor*. We also describe the echolocation calls emitted by members of the taxon in different situations, which may facilitate finding them in previously unsampled locations. Based on the new data, the species occurs from Nepal to North Vietnam and China, which suggests that it could be more widespread than previously thought.

Key words: Indomalayan region, mtDNA, nuDNA, phylogeny, systematics, Vespertilionini

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The taxonomic assignment of *Hypsugo joffrei* (Thomas, 1915) and its presumed allies has long posed a challenge to bat taxonomists. The taxon was originally described from the Kachin Hills of Myanmar (extending as a N–S spine from ca. 27.07°N to 25.47°N at elevations from ca. 400 to 3,411 m a.s.l.) and placed in the genus *Nyctalus* on account of the proportions of the digits. It was subsequently transferred to *Pipistrellus* by Tate (1942), where it was the nominate species of the *Pipistrellus joffrei* group, constituted by *P. anthonyi* (described in the same work), *P. stenopterus*, and *Philetor brachypterus*. Tate (1942:252) also remarked that the group might later be elevated to subgeneric

rank. Ellerman and Morrison-Scott (1951) returned *joffrei* to *Nyctalus* based on the original description, although the authors retained the closely related *anthonyi* in its original genus, *Pipistrellus*. Hill (1966:387), in his review of the genus *Philetor*, followed Tate (1942) in retaining *joffrei* in *Pipistrellus*, and stated that “a review of the structural features of *Philetor* and of other genera and species to which relationship has been postulated hitherto indicates that its affinities are with the *joffrei* group of *Pipistrellus* and with the genus *Tylonycteris*.” The view that *joffrei* belongs in *Pipistrellus* also was accepted by Koopman (1973) and supported by Hill and Harrison (1987), the latter of

whom introduced the *stenopterus* group as part of the subgenus *Hypsugo* of *Pipistrellus* based on the bacular characters of the nominate species, *P. stenopterus*. However, because they were only able to study the penial bone of *stenopterus*, the two other members of this group, *anthonyi* and *joffrei*, were allocated on the basis of craniodental similarities alone. This arrangement was followed by Corbet and Hill (1992), whereas Koopman (1994) placed *joffrei* in *Nyctalus*, together with *anthonyi* and *stenopterus*. Subsequently, Simmons (2005) placed *joffrei* and *anthonyi* in *Hypsugo* and retained *stenopterus* in *Pipistrellus*. On the basis of investigation of all material then available, Saikia et al. (2017) synonymized *anthonyi* with *H. joffrei*. Most recently, however, in detailing the taxonomic status of *Pipistrellus stenopterus*, Kruskop et al. (2018) showed definitively that *stenopterus* and *joffrei* belong to quite distant phylogenetic lineages within the Vespertilioninae, and included molecular data from the mitochondrial *Co1* locus to the effect that separation of *joffrei* from genuine *Hypsugo* was warranted.

Until four specimens were captured in the Hoan Lien Son mountain range of North Vietnam by Kruskop and Shchinov (2010), *H. joffrei* (including *anthonyi*) had been known for almost a century only from Myanmar (Bates et al. 2005). The former authors—based on morphological investigations—noted the ambiguous generic status of the species and called for an in-depth taxonomic reassessment. A further range extension was published by Saikia et al. (2017), who revised the South Asian records of *P. brachypterus* and showed that individuals previously reported from Nepal and Sikkim in fact represented *H. joffrei*. They also reported a new record from Shillong, Meghalaya, India (25.559433°N, 91.89885°E, ca. 1,500 m a.s.l.—Saikia et al. 2017). However, their study excluded material from a Vietnamese expedition that in 2016 collected over a dozen individuals, thereby more than doubling the number of known specimens. Our examination of this new and previously existing material provides novel insights into the phylogenetic relationships, morphometrics, and echolocation call characteristics of this enigmatic taxon. Because the combined evidence indicates a deep divergence between “*H.*” *joffrei* and all other bat taxa presently recognized, we describe herein a new genus for the species.

MATERIALS AND METHODS

Field sampling.—Specimens were collected during a field trip to Mu Cang Chai Nature Reserve, Che Tao commune, Yen Bai Province, Vietnam (21.764465°N, 104.043192°E, 2,038 m a.s.l.) by TG, VTT, and PE. Mist nets stacked vertically to a height of 10 m above ground level across the road that crosses the “Che Tao” mountain range through a mountain pass named “Gate to Heaven” (Cong Troi in Vietnamese). Eighteen individuals of “*H.*” *joffrei* were captured between 25–28 September 2016; several other individuals of the same species (determined on the basis of their size, silhouette, and call characteristics) were observed through the pass during the same period. Identification, determination of sex and age, forearm length, and weight measurements, echolocation recordings, and tissue sampling were undertaken in the field. Five males

and one female were kept as voucher specimens. Wing punches or liver were sampled from the released or euthanized bats, respectively. An additional specimen was captured on 21 March 2017 by NTS in Tay Con Linh Mountain, Vi Xuyen district, Ha Giang Province, Vietnam (22.766°N, 104.816°E, 1,979 m a.s.l.). Field work and handling of bats was undertaken following the guidelines of Sikes et al. (2016), with the permission of Ministry of Agriculture and Rural Development, Hanoi, Vietnam. Specimens are deposited in the collections of the IEBR and the HNHM.

Museum acronyms.—AMNH: American Museum of Natural History, New York, United States; BM(NH): The Natural History Museum, London, United Kingdom, formerly British Museum (Natural History); FMNH: Field Museum of Natural History, Chicago, United States; HNHM: Hungarian Natural History Museum, Budapest, Hungary; IEBR: Institute of Ecology and Biological Resources, Vietnam Academy of Science and Technology, Hanoi, Vietnam; MNHN: Muséum national d’Histoire naturelle, Paris, France; MSB: Museum of Southwestern Biology, University of New Mexico, Albuquerque, United States; NMP: National Museum of Prague, Prague, Czech Republic; RMNH: Naturalis Biodiversity Center, Leiden, The Netherlands, formerly Rijksmuseum van Natuurlijke Historie; ROM: Royal Ontario Museum, Toronto, Canada; ZMB: Museum für Naturkunde, Berlin, Germany, formerly Zoological Museum Berlin; ZMMU: Zoological Museum of Moscow State University, Moscow, Russian Federation; ZSI: Zoological Survey of India, Shillong, India.

Specimens examined.—See Appendix I.

Measurements.—Abbreviations and definitions for external and craniodental measurements are as follows, with mass in grams and all lengths in mm; WT: body mass; FA: forearm length—from the extremity of the elbow to the extremity of the carpus with the wings folded; TIB: tibia length—from the knee joint to the ankle; GTL: greatest length of skull—from the front of the first upper incisor to the most projecting point of the occipital region; STOTL: total length of skull—from the anterior rim of alveolus of the first upper incisor to the most projecting point of the occipital region; CCL: condylo-canine length—from the exoccipital condyle to the most anterior part of the canine; UCCW: width across the upper canines—greatest width across the outer borders of the upper canines; UM3M3W: width across the upper molars—greatest width across the outer crowns of the last upper molars; RW_lac: lacrimal rostrum width—the greatest width of the rostrum between the lacrimal openings; RW_sup: rostrum width at the processus supraorbitale—the greatest width across the supra-orbital tubercles; IOW: interorbital width—least width of the interorbital constriction; ZYW: zygomatic width—greatest width of the skull across the zygomatic arches; MAW: mastoid width—greatest distance across the mastoid region; BCW: braincase width—greatest width of the braincase; BCH: braincase height—from the basisphenoid at the level of the hamular processes to the highest part of the skull, including the sagittal crest (if present); AOB: antorbital width—the distance by which the antorbital foramen is separated from orbit, measured from

the foramen infraorbitale to the foramen lacrimale; UCM3L: maxillary tooththrow length—from the front of the upper canine to the back of the crown of the third molar; UCP4L: upper canine–premolar length—from the front of the upper canine to the back of the crown of the last premolar; MANL: mandible length—from the anterior rim of the alveolus of the first lower

incisor to the most posterior part of the condyle; LCM3L: mandibular tooththrow length—from the front of the lower canine to the back of the crown of the third lower molar; LCP4L: lower canine–premolar length—from the front of the lower canine to the back of the crown of the last premolar; and CPH: least height of the coronoid process—from the tip of the coronoid process to the apex of the indentation on the inferior surface of the ramus adjacent to the angular process. Absolute crown height was used in all height comparisons for individual teeth (e.g., C versus P4).

Color description.—The fur color description was based on digital images using the charts in a ColorChecker Passport (X-Rite, Inc., Grand Rapids, Michigan).

Table 1.—Heterozygous positions in *Rag2* sequences.

Specimen	Position					
	636	662	693	793	831	981
IEBR VN16-170	T	G	A	T	T	T
HNHM 26037	C/T	A/G	A/T	C/T	C/T	C/T
HNHM 26040	C/T	A/G	A/T	C/T	C/T	C/T

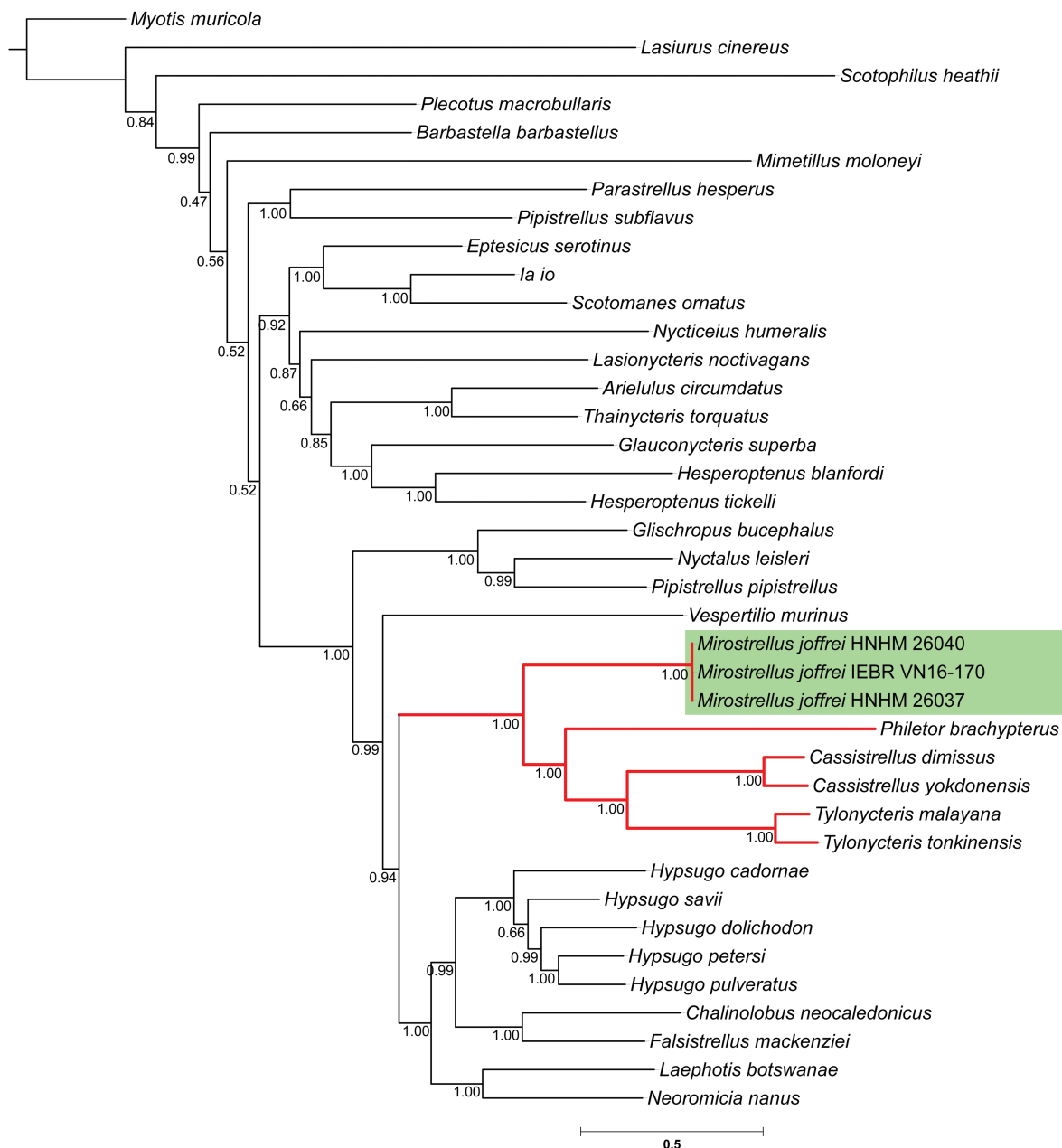


Fig. 1.—Bayesian inference tree based on concatenated sequences (*CoI* + *Cytb* + *Rag2*) of selected species of vespertilionid bats. Numbers at splits indicate posterior probabilities. The black line on the right side of the tree indicates a specific codon insertion in *Rag2* at positions 31–33.

Table 2.—Estimates of genetic distances (GTR model) among sequences, in %. Values in the lower left part of the matrix indicate combined mtDNA differences; upper right values are those of the *Rag2* data set.

Species	1	2	3	4	5	6	7	8
1 <i>Cassidix dimissus</i>		0.69	4.03	3.85	3.85	6.66	2.60	2.78
2 <i>Cassidix yokdonensis</i>	10.02		4.13	3.95	3.95	7.10	3.05	2.98
3 <i>Mirostrellus joffrei</i> IEBR VN16-170	23.65	21.62		0.00	0.00	7.83	5.67	5.36
4 <i>Mirostrellus joffrei</i> HNHM 26037	23.65	21.62	0.00		0.00	7.70	5.53	5.18
5 <i>Mirostrellus joffrei</i> HNHM 26040	23.65	21.62	0.00	0.00		7.70	5.53	5.18
6 <i>Philetor brachypterus</i>	22.59	21.83	19.70	19.70	19.70		6.80	6.67
7 <i>Tylonycteris malayana</i>	20.39	19.94	20.14	20.14	20.14	20.02		0.14
8 <i>Tylonycteris tonkinensis</i>	21.56	21.44	19.94	19.94	19.94	18.95	9.27	

Genetics.—Tissue samples (liver) of voucher specimens were preserved in the field in absolute ethanol and stored in a -80°C freezer at HNHM. Total genomic DNA was extracted with DNeasy Blood & Tissue Kit (QIAGEN, Hilden, Germany) according to the instructions of the manufacturer. For phylogenetic analysis, mitochondrial (hereafter mtDNA) Cytochrome c oxidase subunit I (*Co1*, 657 bp) and Cytochrome *b* (*Cytb*, 1,140 bp), and the Recombination activating gene 2 (*Rag2*, 1,151 bp) nuclear gene were amplified with primers VF1d/VR1d (Ivanova et al. 2007), Molcit-F/Cytb-H (Ibáñez et al. 2006; Weyeneth et al. 2008), and 179F/1458R (Stadelmann et al. 2007), respectively. PCR reactions followed Stadelmann et al. (2007), Csorba et al. (2015), and Lim et al. (2016).

Three “*H.*” *joffrei* and one *Vespertilio murinus* specimen were sequenced for *Co1*, *Cytb*, and *Rag2* genes; the relevant sequences are deposited in GenBank (accession numbers: MN813969–MN813980); additional pertinent GenBank sequences also were downloaded. Species were selected to represent all major groups within Vespertilioninae as defined by Amador et al. (2018), Koubínová et al. (2013), and Roehrs et al. (2010), including all available species from the hypsigene-group sensu Roehrs et al. (2010). Only species with all three gene sequences available were included in our analyses, and *Myotis muricola* was used as the outgroup (Appendix II).

Sequences were aligned in MEGA X v10.0.5 (Kumar et al. 2018); missing nucleotides were filled with “N”s, insertions in *Rag2* sequences were excluded, and longer sequences truncated to the following lengths: *Co1*—657 bp; *Cytb*—1,140 bp; and *Rag2*—1,017 bp. Separate (*Co1*, *Cytb*, and *Rag2*) as well as concatenated (mtDNA + *Rag2*) trees were generated using Bayesian inference method (BI). MrBayes v3.2.6 (Ronquist et al. 2012) was run on the CIPRES Science Gateway (Miller et al. 2010) for 10 million generations, sampling every 1,000 generations. Model parameters for single gene trees were determined with jModelTest2 (Darriba et al. 2012) with the following results: *Co1*—HKY + G + I; *Cytb*—GTR + G + I; and *Rag2*—GTR + G + I. For the concatenated tree, model parameters *Co1* pos 1—GTR + GI, pos 2—F81 + PI, pos 3—GTR + G; *Cytb*: pos 1–3—GTR + GI; *Rag2* pos 1–2—GTR + GI, pos 3—GTR + G were used, as determined using PartitionFinder2 (Lanfear et al. 2017). Ten percent of the generations were treated as burn-in and discarded. Posterior probabilities were calculated from the consensus of the remaining trees. Two parallel runs were performed on each data set and results were combined. According to Tracer v1.7.1 (Rambaut et al. 2018),

Table 3.—Selected external and craniodental measurements (in mm) of *Mirostrellus joffrei* specimens. Values are given as mean \pm SD; min–max (*n*). Acronyms and definitions for measurements are given in the text.

Character	Measurement
WT	16.0 \pm 1.95; 13.0–19.0 (18)
FA	38.6 \pm 1.08; 35.7–40.2 (28)
TIBIA	15.4 \pm 0.74; 13.8–16.4 (12)
GTL	15.33 \pm 0.27; 14.86–15.77 (12)
STOTL	14.91 \pm 0.30; 14.47–15.35 (15)
CCL	14.21 \pm 0.24; 13.65–14.72 (17)
UCCW	5.15 \pm 0.11; 4.96–5.34 (16)
UM3M3W	7.08 \pm 0.15; 6.79–7.34 (18)
RW_lac	7.25 \pm 0.61; 6.67–8.59 (18)
RW_sup	8.04 \pm 0.35; 7.62–8.62 (10)
IOW	4.68 \pm 0.17; 4.34–5.02 (20)
ZYW	10.47 \pm 0.31; 9.95–10.99 (13)
MAW	8.90 \pm 0.18; 8.58–9.28 (17)
BCW	8.04 \pm 0.25; 7.64–8.58 (17)
BCH	5.57 \pm 0.19; 5.36–6.00 (10)
AOB	0.55 \pm 0.18; 0.36–0.86 (14)
UCM3L	5.19 \pm 0.06; 5.12–5.30 (16)
UCP4L	2.05 \pm 0.07; 1.90–2.18 (13)
MANL	10.89 \pm 0.25; 10.53–11.45 (19)
LCM3L	5.55 \pm 0.10; 5.29–5.70 (19)
LCP4L	1.66 \pm 0.17; 1.44–1.80 (4)
CPH	3.66 \pm 0.10; 3.54–3.90 (14)

the likelihood scores were stabilized and the effective sample size (ESS) values were significantly higher than 200 in each run. Trees were edited with iTOL v3 (Letunic and Bork 2016). Pairwise distances were calculated using GTR model in case of concatenated mtDNA (*Co1* + *Cytb*) and *Rag2* sequences in PAUP* 4.0a (Swofford 2003).

Acoustic analyses.—The echolocation calls of captured bats were recorded in a flight tent (3 \times 5 \times 1.5 m; four individuals) and during hand release (nine individuals). In addition, calls of free-flying bats (*n* = 8) also were sampled at the capture site. Our recordings were made using a Pettersson D1000X detector (Pettersson Elektronik AB, Uppsala, Sweden) in manual mode, with a sampling rate of 500 kHz. Sound analyses were carried out using BatSound 4.2. (Pettersson Elektronik AB, Sweden), using the following settings: FFT size = 512, overlap = 96%, Hanning window.

We selected one typical signal of each call type from individual sequences to avoid pseudo-replication. The following parameters were measured from each of the selected calls: call duration, T_{dur} (duration of a single pulse); pulse interval, PI (time from the start of one call to the beginning of the next);

start frequency, F_{start} (frequency value at the start of the call); end frequency, F_{end} (frequency value at the end of the call); frequency with maximum energy, F_{maxE} (frequency of maximum energy for the whole call). Bandwidth was calculated from F_{start} and F_{end} values. Pulse duration, starting and terminal frequencies were determined where the signals were clearly above the background noise levels.

RESULTS

Morphology.—Based on detailed comparisons of all “*H.*” *joffrei* specimens currently known with morphologically similar or phylogenetically closely related species in South-East Asia (including available holotypes), we identified the following unique combination of external and craniodental features that this species possesses: conspicuous coloration of dorsal and ventral fur, shortened fifth finger, poorly developed calcar lobe, developed supraorbital tubercles, strongly bicuspid upper canine, and myotodont lower molars (postcrisid linking to the entoconid). Taken together, these features strongly suggest the taxon can be

distinguished at the level of genus from all other bat taxa currently recognized.

Genetics.—No intraspecific variability was detected in mtDNA of “*H.*” *joffrei*, although there existed differences among *Rag2* sequences (Table 1) that did not result in amino acid changes. Specimens HNHM 26037 and 26040 had several heterozygous nucleotide positions, and the chromatogram of the IEBR VN16-170 *Rag2* sequence lacked double peaks.

Concatenated (Fig. 1) and separate *Co1*, *Cytb*, and *Rag2* trees (Supplementary Data SD1) show that “*H.*” *joffrei* is only distantly related to the strongly supported monophyletic *Hypsugo* (sensu stricto) clade, and instead groups with *P. brachypterus*, *Cassistrellus* spp., and *Tylonycteris* spp. Comparing *Rag2* sequences, “*H.*” *joffrei* has an insertion (CAA, Glutamine) at the positions 31–33 of the sequence, hence the total length is 1,151 bp. The same inserted codon is present in *Cassistrellus* spp., *P. brachypterus*, *Pipistrellus pipistrellus*, and *Tylonycteris* spp., further supporting the monophyly of this clade.

In mtDNA, *P. brachypterus* was the most similar to “*H.*” *joffrei*, with a genetic distance of 19.7%, whereas in *Rag2*,



Fig. 2.—Habitus of a live adult female *Mirostrellus joffrei* from Mu Cang Chai, Vietnam (HNHM 26034). Note the coloration of the dorsal and ventral side, which is unique for this species.

Cassistrellus spp. were the closest, with a sequence divergence of 3.85–3.95% (Table 2).

Based on the phylogenetic reconstructions, which are fully supported by anatomical traits, “*H.*” *joffrei* is separable at the level of genus both from *Hypsugo* as well as all other bat genera.

Mirostrellus gen. nov.

Type species.—*Nyctalus joffrei* Thomas, 1915.

Etymology.—From the Latin “*mirus*” meaning “surprise, marvel,” which reflects that both the systematic position and the wide distribution of this bat (previously thought to be extremely rare) were pleasant surprises for the authors.

Diagnosis.—A medium-sized vespertilionid, with a FA of 35.7–40.2 mm. The fifth finger of the wing is shortened (on average 20 mm shorter than the fourth finger) and the pelage is sparse and velvety. The supraorbital tubercles are well-developed, protruding for 1.47–1.76 mm measured from the lachrymal opening; the sagittal crest is barely visible, being

only approximately 0.1 mm high. The upper canine is characterized by a developed posterior secondary cusp. The taxon has two upper and lower premolars and its lower molars are myotodont.

Description.—The only known species of the genus, *Mirostrellus joffrei*, has a FA between 35.7–40.2 mm, CCL 13.65–14.72 mm, and UCM3L 5.12–5.30 mm (Table 3). The body is covered with moderately long (5.5–7.5 mm on the back and 4.5–5.4 mm on the ventrum) and sparse velvety fur. On the dorsum the lower portion of individual hairs is dark black (PANTONE 440 C), whereas the upper section gradually lightens to warm brownish black (PANTONE 411 C); the overall impression is brownish black (PANTONE 412 C). On the ventral surface the individual hair is uniform sandbrown (PANTONE 728C; Fig. 2). Wings and hindfoot are black. The muzzle blunt and massive (12–14 mm wide), with pronounced buccal glands. The ears are broad (7.5–9.5 mm in width) and rounded, 11–14 mm in length, and have a pale antitragal lobe (Fig. 3). The tragi are short (2.1–3.0 mm) and broad



Fig. 3.—Close up of the head of an adult male *Mirostrellus joffrei* from Mu Cang Chai, Vietnam (HNHM 26040).



Fig. 4.—Penis of *Mirostrellus joffrei* from Mu Cang Chai, Vietnam (HNHM 26041). Not to scale.

(2.0–2.9 mm) and turned forward, so their upper half appears much wider than the lower portion. The wings are narrow (a common feature for fast-flying bats, i.e., *Mimetillus*, *Philetor*, and *Nyctalus*), the third finger is about 21–23 mm longer than the fifth (which itself is 37–43 mm in length), aspect ratio is 2.4–2.6. In the tail, only distal half of the last vertebra emerges for 1.0–2.5 mm from the uropatagium. The calcars are extending less than half of the free margin of the tail membrane and distally bear a narrow and elongated (1.2–1.5 mm wide and 4.21–5.38 mm long) calcar lobe.

Both the male and female external genitalia are similar to those of *Philetor*. The penis has a complex structure with a long shaft, which on the dorsal surface bears a cushion-like pad divided by a longitudinal median depression, and a separated, prominent glans (Fig. 4). The female external genitalia is similarly complicated, the transverse vulval opening is separated from the anus by a swollen perineal pad, and is anteriorly almost fully concealed by a wide, triangular cushion. The vulva itself is anteriorly prolonged as a narrow slit.

The skull has distinct supraorbital projections that protrude beyond the outline of the skull (Figs. 5–7). The occiput is abruptly elevated and its upper point is turned somewhat forward against the condyles. The opening of the antorbital canal is situated just behind the level of the first root of M1. The lacrimal foramen is well-developed and close to the antorbital one, being divided from the latter by a thin bony wall. The anterior palatal emargination is heart-shaped, and protrudes backward to the middle of the upper large

premolars. The posterior palatal emargination has a pointed middle projection. The basal pits are well-demarcated. The sagittal crest is very low but present, and anteriorly is continuous with the similarly weakly developed supraorbital crests. The mandible is moderately robust, with a long angular process that is curved distally. The coronoid process is moderately high (3.54–3.90 mm).

The dental formula is I2 C1 P2 M3/i3 c1 p2 m3 × 2 = 34. The inner upper incisors are clearly bicuspidate and the outer incisors (I3) do not reach the height of the secondary cusp of I2. The upper canine is large, with a well-developed secondary cusp on the posterior blade. The anterior upper premolar is minute and is displaced lingually from the toothrow, hence in lateral view totally obscured by the canine's cingulum. Due to the greatly reduced hypocones of M1 and M2 (height and basal dimensions are nearly the half those of the corresponding protocones) the trigon basins of these teeth are nearly open. The cusps of the lower incisors are arranged into a single row. The lower molars are clearly myotodont and their talonids are about one and half times larger than the corresponding trigonids. The lower premolars are similar in shape and size.

The baculum (Fig. 8) is about 1 mm in total length and 0.75 mm in maximum width; the main shaft is narrow (0.14–0.20 mm) and straight. The distal tip is blunt, semicircular, whereas the basal portion has well-developed lateral projections angling at 130° and 230° from the shaft approximately 0.6 mm from the distal tip; the emarginations are somewhat downwardly curved (ca. 140°) and divided by a wide basal emargination, ca. 0.5 mm wide and 0.3 mm deep. The urethral groove on the main shaft is present but very shallow.

Comparisons.—Because *M. joffrei* was initially described as a *Nyctalus*, and later associated with *Pipistrellus* and *Hypsugo*, but is phylogenetically close to *Philetor*, *Cassistrellus*, and *Tylonycteris*, we compare it below in detail with these taxa.

Mirostrellus gen. n. can be distinguished from all species of *Pipistrellus* and *Nyctalus* by its poorly developed calcar lobe which lacks a central supporting cartilage, relatively high mandibular coronoid process (over 3.5 mm versus less than 3.3 mm height in the externally similar sized *Pipistrellus* species and in the even larger *N. leisleri* and *N. azoreum*) and myotodont (versus nyctalodont) lower molars. Among the South-East Asian *Pipistrellus* species, *Mirostrellus* gen. n. is most similar to *P. stenopterus*, from which it can be further distinguished by its flat rostral profile and very low cranial crests (versus convex rostral profile and well-pronounced sagittal crest in *P. stenopterus*; Fig. 6c).

It differs externally from *Hypsugo* in having a swollen muzzle (Fig. 3) due to the developed buccal glands, and with only half of the last vertebra protruding from uropatagium (in *Hypsugo* the whole last vertebra is free from the membrane), very shallow urethral groove and developed lateral basal lobes of the baculum (as compared with the typical *Hypsugo* bacula, see, i.e., figure 6a, 8a, b, c, e, f, in Hill and Harrison 1987), developed supraorbital tubercles, and a strongly bicuspid upper canine.

Compared with *Philetor*, *Mirostrellus* gen. n. has a differently shaped baculum (Fig. 8) without the enlarged tip and

the elongated, dorsoventrally strongly curved shaft typical of *Philetor* (see figure 1 in Hill 1966). The female external genitalia of the new genus is less complex as compared with *Philetor* (Hill 1966: figure 2) with both the anterior and posterior perineal pads are undivided. *Mirostrellus* gen. n. also has conical upper incisors and a basally nearly quadratical posterior premolar (*Philetor* is characterized by a blade-like first upper incisor and anterioposteriorly strongly compressed P4 the length of which is equal to approximately one-half of its width), longer toothrow (UCM3L 5.12–5.30 mm versus 4.42–4.98 mm; LCM3L 5.29–5.70 mm versus 4.72–5.22 mm), and myotodont (versus nyctalodont) lower molars.

In contrast with *Cassistrellus*, *Mirostrellus* gen. n. is smaller in several dental measurements (UCM3L 5.12–5.30 mm versus 5.8–6.6 mm, LCM3L 5.29–5.70 mm versus 6.29–7.05 mm), has a very low sagittal crest, and lacks an occipital helmet

(formed by the well-developed sagittal and lambdoid crests, which meet near the top of the skull in *Cassistrellus*). It also possesses a second (anterior) upper premolar.

With respect to the closely related *Tylonycteris*, *Mirostrellus* gen. n. can be distinguished by its much larger size (FA 35.7–40.2 mm versus 24.4–32 mm, CCL 13.65–14.72 mm versus 9.72–11.82 mm, UCM3L 5.12–5.30 mm versus 3.27–4.31 mm) absence of adhesive disks on pollex and heels, nonflattened skull (Fig. 6a versus 6g), and by the presence of the small upper premolar.

From all other more distantly related Indomalayan Vespertilioninae genera, *Mirostrellus* gen. n. can generally be distinguished by its shortened fifth finger (where the combined length of the fifth metacarpal and the first phalanx is subequal with the length of the third metacarpal) and the presence of a secondary cusp on the upper canine.

Acoustics.—Our sample bats produced different calls depending on the behavior being recorded (Table 4). In the

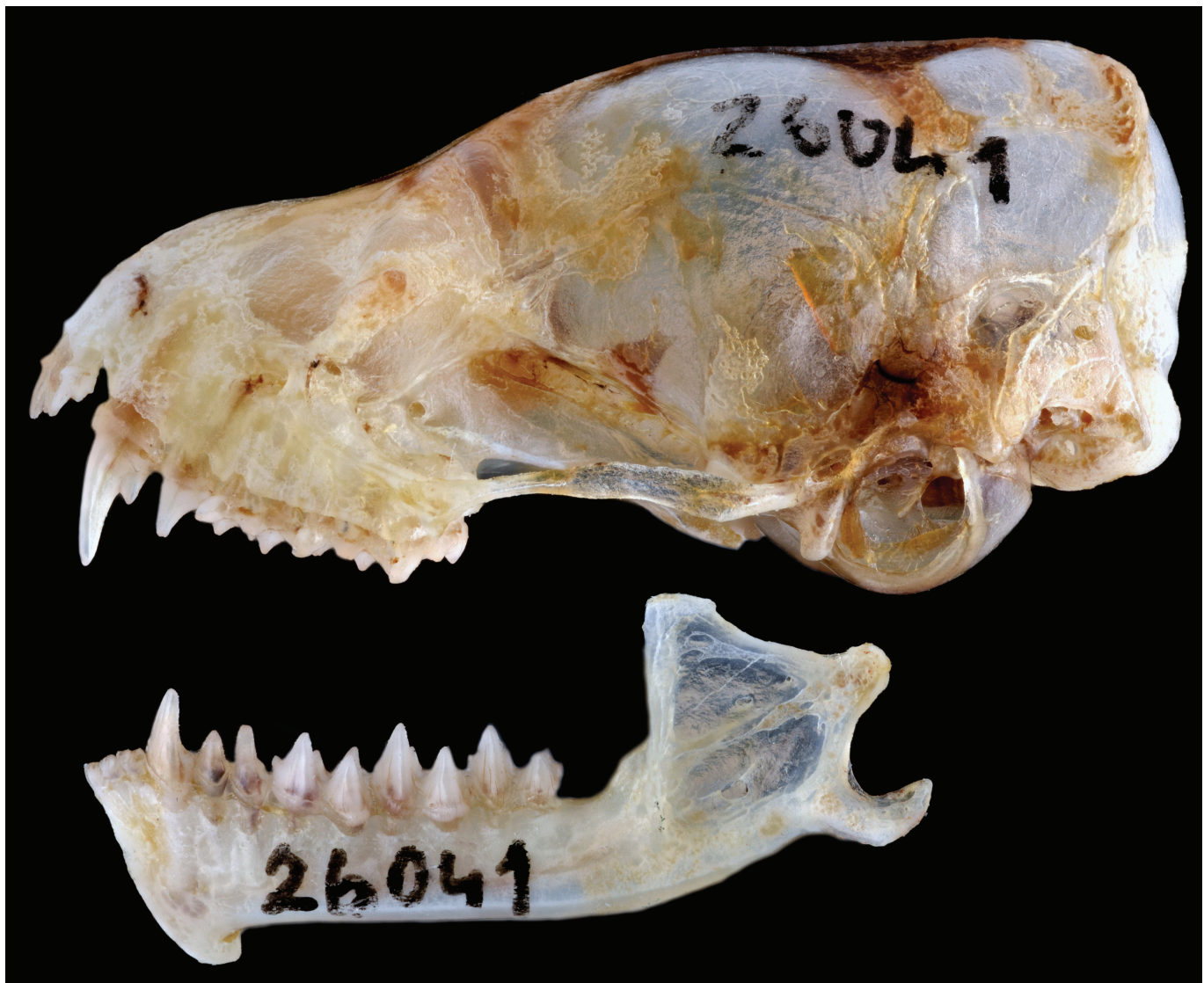


Fig. 5.—Lateral view of skull of *Mirostrellus joffrei* from Mu Cang Chai, Vietnam (HNHM 26041).

flight tent, *M. joffrei* emitted very short ($T_{dur} = 2.7 \pm 1.5$ ms) frequency-modulated (FM type) calls with short pulse intervals (PI = 69.5 ± 27.5 ms) and highest observed frequencies (F_{maxE}) of 39.0 ± 2.3 kHz from the three different recording situation. In case of hand releases, they emitted calls with a steep frequency-modulated beginning and a short, quasi-constant frequency ending (FMQCF type) which had lower frequencies ($F_{maxE} = 34.6 \pm 1.2$ kHz) and longer durations ($T_{dur} = 6.4 \pm 2.1$ ms) and pulse intervals (PI = 90.3 ± 10.8 ms) than calls recorded in flight tents. The calls of free-flying individuals were mainly FMQCF in structure (Fig. 9), although in some cases the FM part was significantly reduced, resulting in a near QCF structure. The FMQCF calls of free-flying individuals had clearly higher frequency values ($F_{maxE} = 30.5 \pm 0.7$ kHz) and shorter durations ($T_{dur} = 11.8 \pm 1.6$ ms) and pulse intervals (PI = 158.4 ± 36.9 ms) than the QCF calls ($F_{maxE} = 28.3 \pm 0.6$ kHz, $T_{dur} = 13.3 \pm 2.1$ ms, PI = 199.8 ± 36.2 ms). This call structure is typical for aerial-hawking species that forage in open and edge spaces.

Geographic distribution.—The only known species of *Mirostrellus* gen. n. has an Indomalayan distribution, ranging

from Nepal, NE India (Sikkim, Meghalaya), through the northern part of Myanmar, to North Vietnam (Saikia et al. 2017). In the National Museum of Prague (Czech Republic), four hitherto unreported specimens from western Yunnan, China (Zao Teng He, 25.31°N , 98.80°E , 1,451 m a.s.l.), were revealed by SVK. The species probably also occurs between these localities as it is difficult to capture and so may be missed during faunal surveys (Fig. 10).

Habitat and ecology.—The recent observations from Vietnam provide new insights into the habitat requirements and ecology of this very poorly known bat. All collecting sites (Mu Cang Chai, Tram Ton [22.35°N , 103.77°E , 1,850–1,950 m a.s.l.]; Cat Cat [22.33°N , 103.83°E , 1,290 m a.s.l.]; Tay Con Linh) are located in the high mountains of northern Vietnam. The mean annual temperature of these sites is usually lower than 20°C , and mean precipitation usually over 1,700 mm. In these areas, temperatures can fall below freezing during the coldest days of the winter, usually in December and January. The vegetation of collection sites consists of montane evergreen forests. In Mu Cang Chai and Tay Con Linh, the mature and least disturbed forests are found only at high elevations, whereas little forest

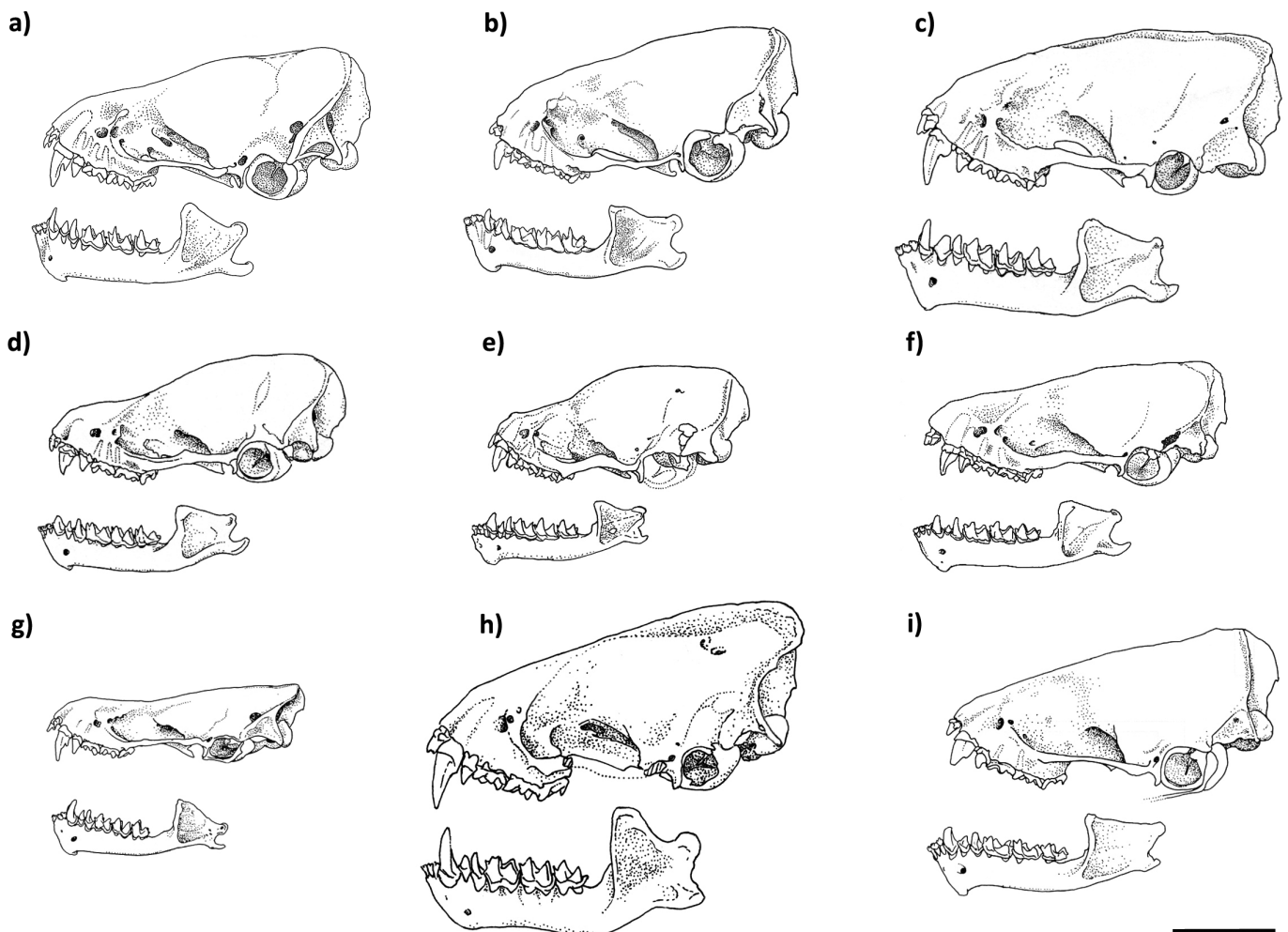


Fig. 6.—Lateral views of skulls of a) *Mirostrellus joffrei* (ZMMU S-186691); b) *Philetor brachypterus* (ROM 102019); c) *Pipistrellus stenopterus* (ZMMU S-103149); d) *Hypsugo pulveratus* (ZMMU S-167186); e) *H. macrotis* (MHNG 1486.94); f) *H. alaschanicus* (ZMMU S-108373); g) *Tylonycteris malayana* (ZMMU S-186637); h) *Cassistrellus dimissus* (MHNG 1926.053); i) *Nyctalus leisleri* (ZMMU S-176068). Scale bar = 5 mm.

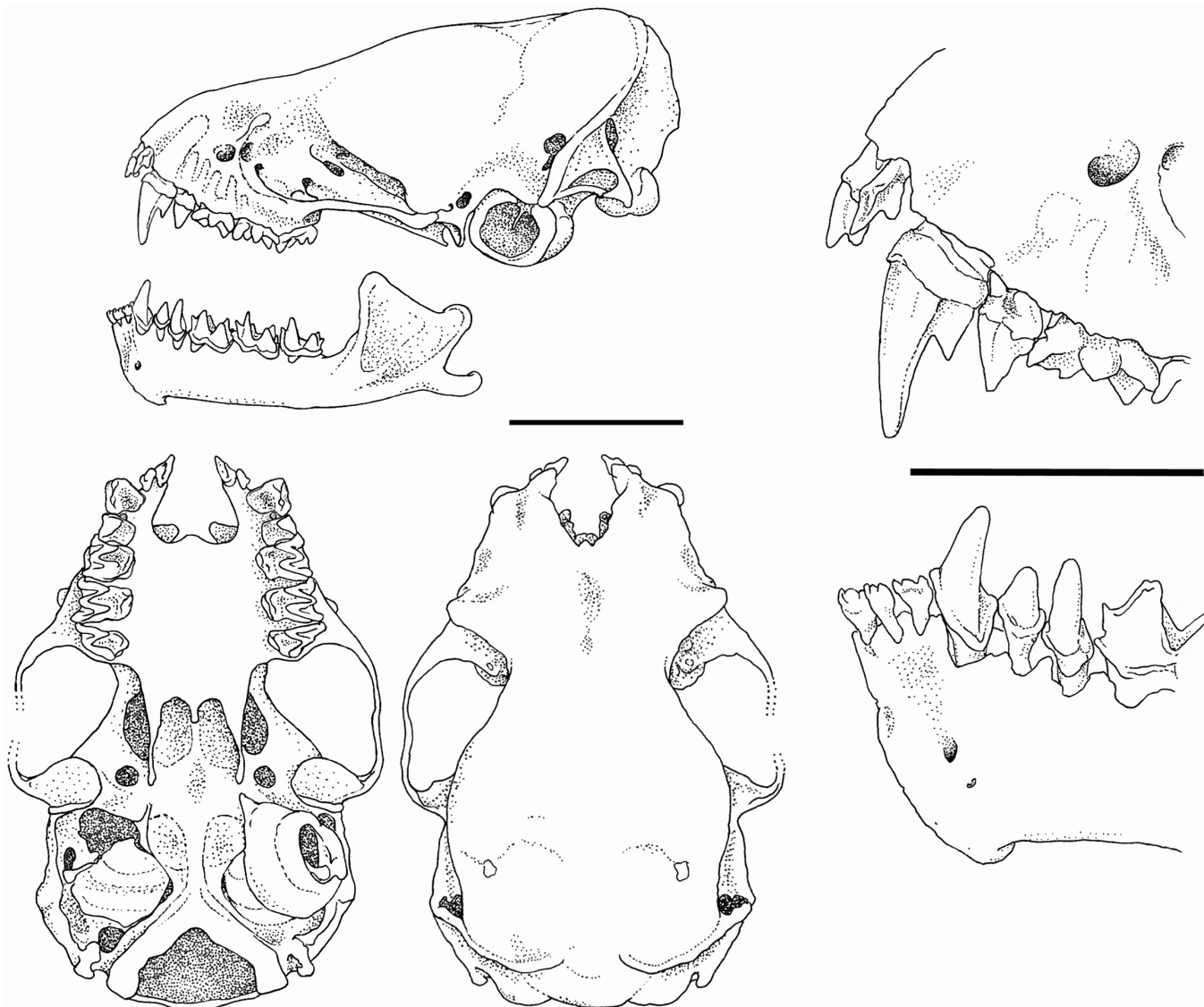


Fig. 7.—Dorsal, ventral, and lateral views of the skull and mandible of a male *Mirostrellus joffrei* from Tram Ton forest station, Vietnam (ZMMU S-186691). Scale bar =5 mm.

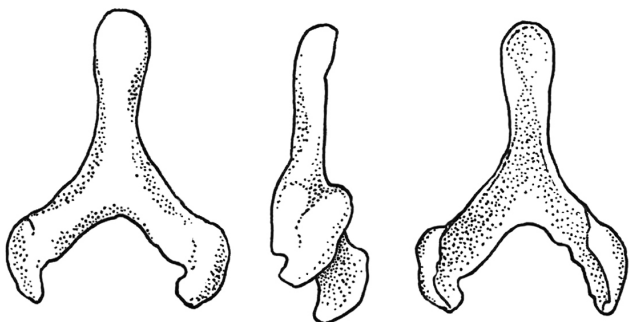


Fig. 8.—Baculum of *Mirostrellus joffrei* from Tram Ton forest station, Vietnam (ZMMU S-186692). Scale bar =1 mm.

remains at lower parts. All of the records are from higher elevations, between 575 and 2,038 m a.s.l., but mostly (nine of 11 known) above 1,000 m a.s.l.

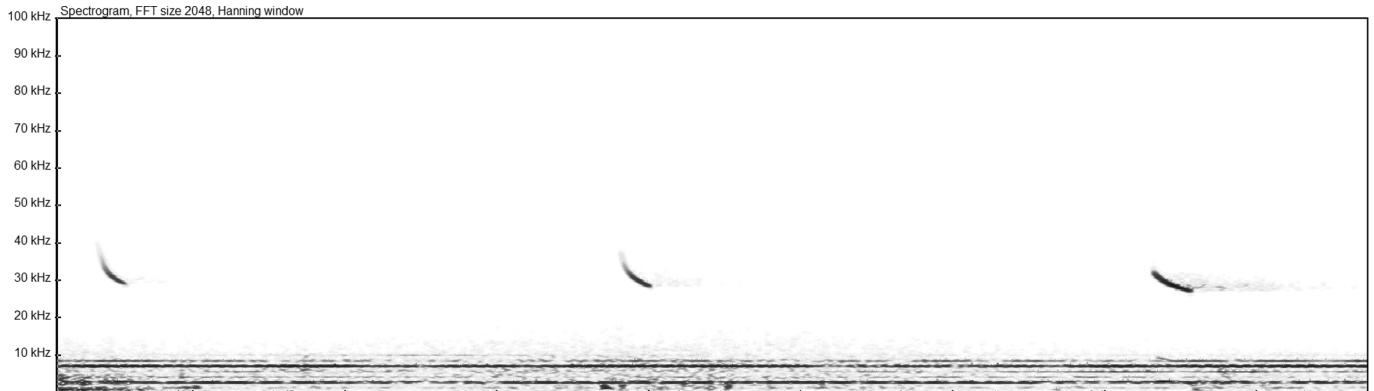
In Tram Ton, bats (males only) were captured over a stream at the elevation of ca. 1,900 m a.s.l. in tall primary mountain forest. Other fast-flying bats such as *Miniopterus fuliginosus* also were observed in that location.

The site in the vicinity of Cat Cat village is situated at ca. 1,290 m a.s.l. and is mostly deforested. *Mirostrellus joffrei* were seen here at dawn, foraging 10–20 m above ground level; they resembled small noctules in their flight behavior. The single specimen collected was an adult female. The only other bats observed simultaneously at that location were *Pipistrellus coromandra*.

The specimen (adult male) from Tay Con Linh was captured in a primary forest with trees ranging from 15 to 20 m. Other bats captured at the same locality were: *Myotis altarium*, *Coelops frithii*, *Rhinolophus affinis*, *Arielulus circumdatus*, *Harpicephalus harpia*, *Murina huttoni*, *Murina chrysochaetes*, and *Harpiola isodon*.

Table 4.—Acoustic parameters. Acronyms and definitions for measurements are given in the text.

Settings	Call type	<i>n</i>		F_{start} (kHz)	F_{maxE} (kHz)	F_{end} (kHz)	T_{dur} (ms)	PI (ms)	BW (kHz)
Flight tent	FM	4	Mean \pm <i>SD</i>	66.8 \pm 7.8	39.0 \pm 2.3	32.8 \pm 2.1	2.7 \pm 1.5	69.5 \pm 27.5	34.0 \pm 8.7
			Min–max	59.6–77.2	36.5–41.4	29.9–34.9	1.5–4.8	37.6–103.0	24.7–43.9
Hand release	FMQCF	9	Mean \pm <i>SD</i>	61.8 \pm 7.8	34.6 \pm 1.7	31.2 \pm 1.4	6.4 \pm 2.1	90.3 \pm 10.8	30.7 \pm 7.5
			Min–max	51.1–72.4	33.1–38.1	29.4–33.4	2.2–8.0	71.6–107.0	20.7–41.8
Free-flying	FMQCF	8	Mean \pm <i>SD</i>	42.4 \pm 4.5	30.5 \pm 0.7	28.8 \pm 0.9	11.8 \pm 1.6	158.4 \pm 36.9	13.6 \pm 3.9
			Min–max	36.3–50.0	29.5–31.4	27.4–29.6	10.0–14.6	93.3–187.0	8.8–20.4
Free-flying	QCF	4	Mean \pm <i>SD</i>	32.2 \pm 1.3	28.3 \pm 0.6	26.7 \pm 0.8	13.3 \pm 2.1	199.8 \pm 36.2	5.5 \pm 1.0
			Min–max	30.4–33.4	27.5–28.7	25.8–27.8	11.3–16.0	175.6–253.6	4.6–6.8

**Fig. 9.**—Echolocation call sequence of a free-flying *Mirostrellus joffrei* from Mu Cang Chai, Vietnam.

Mirostrellus joffrei is probably a forest-dwelling species given that most of the individuals in Mu Cang Chai were caught just after sunset (ca. 1800 h local time) and no caves or other underground shelters are known in the vicinity, although rock crevices could occur in nearby granite formations. However, *Hypsugo cadornae* and *H. pulveratus* were captured in the same mist nets; and these species are thought to primarily roost in caves. Judging from its body and wing proportions, *M. joffrei* is a fast-flying aerial-hawker; this corresponds with our field observations and the characteristics of echolocation calls produced by free-flying individuals. Like the similarly built noctules, it may make long-range flights to locate high concentrations of night-flying insects.

DISCUSSION

Frequent nomenclatural changes for a given taxon are suggestive of uncertain and likely imperfect taxonomy which—after careful examination and combination of different approaches—can result in novel systematic arrangements (i.e., Górföl and Csorba 2018; Ruedi et al. 2018). In the case of Joffre's Pipistrelle, integrative taxonomy, including comparative morphology, morphometrics, and multi-locus sequence typing, allowed us to reconstruct the phylogenetic position of this very poorly known bat and to distinguish it from all other currently recognized genera.

Amador et al. (2018) identified a clade in the Vespertilionini that contained *Philetor* and *Tylonycteris*. That same clade also was recovered by Ruedi et al. (2018) with the addition of

Cassistrellus, a then newly described genus of vespertilionid. *Mirostrellus* gen. n. is included in this group with high support on the basis of phylogenetic reconstructions. The common features of taxa belonging to this group (all of which are fast-flying aerial-hawkers) are as follows: short tragus, fleshy posterior edge of ear conch that extends toward the corner of mouth, prominent facial glands, developed supraorbital processes, upper canines that tend to have an additional cusp (exception is *Cassistrellus*), and a special insertion in the *Rag2* gene at positions 31–33.

The individuals that were captured and observed during the expedition to Mu Cang Chai provided a unique opportunity to study the echolocation calls of the species under different conditions: in a flight tent, in hand-released individuals, and in free-flying bats. Our description of its call parameters will assist detection of this rarely encountered species in new areas. This is important because the species is difficult to catch with mist nets or harp-traps due to its behavior of fast-flying and foraging at great heights (Kruskop and Shchinov 2010; our personal observations). Thus, our ability to record the species will largely rely on acoustic surveys. Besides the two abovementioned *Hypsugo* species, other rarely mist-netted bats including *Thainycteris aureocollaris*, *Nyctalus plancyi*, *Ia io*, *A. circumdatus*, and *Scotomanes ornatus*, as well as other, more common, aerial-hawkers such as *Taphozous melanopogon* and *M. fuliginosus*, also were recorded during our six nights of fieldwork at Mu Cang Chai. This is evidence that passes in large and steep mountain ranges function as important commuting paths between roosts and foraging areas on opposing

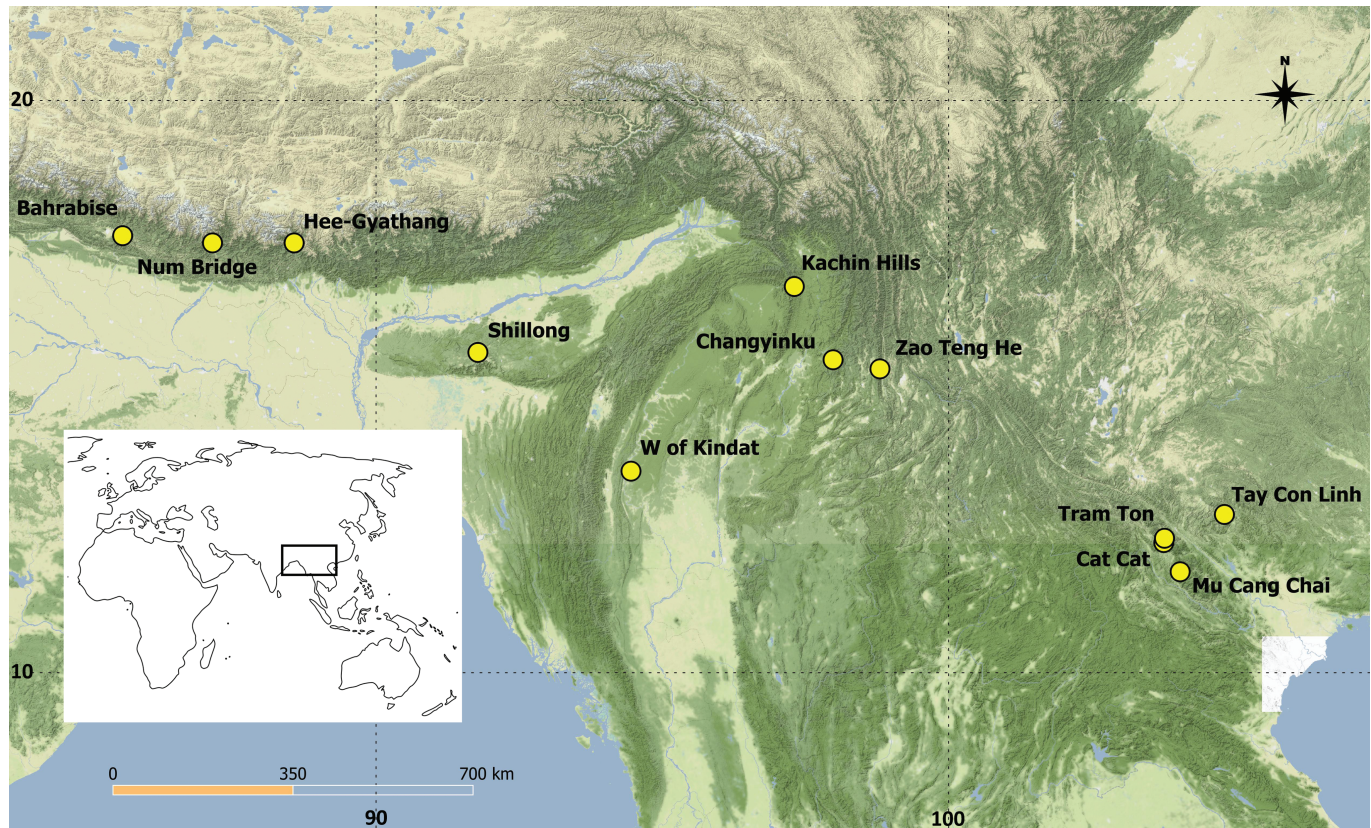


Fig. 10.—Distribution map of *Mirostrellus joffrei*.

mountain sides and provide ideal locations to study bats that otherwise are hard to observe.

The current IUCN Red List status for “*Hypsugo*” *joffrei* is Data Deficient (Görföl et al. 2016). Because the new localities are fairly close to the previous recorded localities (Hoang Lien Son mountain range is about 40 km from Mu Cang Chai and 120 km from Tay Con Linh, whereas Kachin Hills is in the vicinity of the locality in Yunnan, China), the species’ known distribution area has not changed considerably. Furthermore, while the number of individuals encountered during our expedition was relatively high, the species remains known only from a handful of localities. Our knowledge about its ecology, habitat preferences, and conservation status, therefore, remains largely incomplete. As a consequence, we believe that its present IUCN status should be retained.

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SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Bayesian inference tree based on a) *Col1*, b) *Cytb*, c) *Rag2* sequences of selected species

of vespertilionid bats. Numbers at splits indicate posterior probabilities.

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APPENDIX I SPECIMENS EXAMINED

Cassidix dimissus—THAILAND: Surat Thani Province; Kao Nawng, Tai Rom Yen National Park, 427 m: BM(NH) 1916.4.21.1 (holotype). LAOS: Phongsaly Province; Ban Naten, Nam Lan Conservation Area: MHNG 1926.053.

Cassidix yokdonensis—VIETNAM: Dak Lak Province; Yok Don National Park, Dak Ken River (tributary of the Serepok River), base of Yok Mt., 12.8672N, 107.7075E, 194 m: ROM 107751 (holotype).

“Hypsugo” joffrei—CHINA: Yunnan Province; Zao Teng He, 25.31N, 98.80E, 1,451 m: NMP CN007, CN008, CN009, CN010. INDIA: Meghalaya State; Shillong, Risa Colony area, 25°33.566'N, 91°53.931'E, 1,500 m: ZSI V/M/ERS/292. INDIA: Sikkim State; Hee-Gyathang, 27°30'N, 88°30'E, 1,846 m: MSB 67466, 67467. MYANMAR: Kachin State; Changyinku, Chipwi River Valley, 2,134 m: AMNH 114849 (*anthonyi* holotype). MYANMAR: Kachin State; Kachin Hills: BM(NH) 1888.12.1.37 (holotype). MYANMAR: Chin State; Chin Hills: BM(NH) 1916.3.26.2. MYANMAR: Sagaing State; W of Kindat: BM(NH) 1916.3.26.83, 1916.3.26.84. NEPAL: Sindhupalchok District; Bhabise, approx. 27°78'N, 85°89'E, 575 m: FMNH 114249. NEPAL: Sankhuwasabha District; Num Bridge, approx. 27°54'N, 87°34'E, 850 m: FMNH 114481. VIETNAM, Yen Bai Province, Che Tao commune, Mu Cang Chai Nature Reserve, 21.764465°N, 104.043192°E, 2,038 m: HNHM 26037, 26040, 26041; IEBR VN16-168, VN16-169, VN16-170. VIETNAM: Ha Giang Province; Vi Xuyen District, Tay Con Linh Mountain, 22.766°N, 104.816°E, 1,979 m: IEBR M-6516. VIETNAM: Lao Cai Province; Sa Pa, Tram Ton forest station, 22.35°N, 103.77°E, 1,850–1,950 m: ZMMU S-186691, 186692, 186693. VIETNAM: Lao Cai Province; Sa Pa, Cat Cat, 22.33°N, 103.83°E, 1,290 m: ZMMU 186694.

Hypsugo affinis—CHINA, Yunnan Province, Lijiang: AMNH 44565. INDIA: Uttarakhand State; Kumaon: BM(NH) 1879.11.21.103. INDIA: Kerala State; Wynaad (now Wayanad?): 1982.3.3.2. INDIA: Tamil Nadu State; Nilgiris District, Kotagiri: BM(NH) 1892.4.7.1, 1892.4.7.2. INDIA: West Bengal State; Darjeeling, Gopaldhara: BM(NH) 1916.3.25.5. NEPAL: Central Nepal; Bhaktapur, Nagarkot: BM(NH) 1937.3.14.3.

Hypsugo alashanicus—RUSSIA: Primorskiy Territory; Khasan District, Slavyanka: ZMMU S-108373.

Hypsugo cadornae—INDIA: West Bengal State; Darjeeling, Pashok: BM(NH) 1916.3.25.6 (holotype).

Hypsugo dolichodon—LAOS: Attapu Province; 10 km east from Ban Paam, Xe Kaman proposed dam site, 14°57'N, 107°08'E, 150 m: ROM 110459 (holotype), 110462 (paratype). LAOS: Attapu Province; 14°58'N, 107°13'E, 150 m: ROM 110464 (paratype). VIETNAM: Dong Nai Province; Cat Tien National Park, 11°25'N, 107°26'E, 100 m: ZMMU S-180563, 180565.

Hypsugo imbricatus—INDONESIA: Java. BM(NH) 1879.11.21.108 (holotype).

Hypsugo kitcheneri—INDONESIA, Borneo, Central Kalimantan, Boentok, Barito River: BM(NH) 1910.4.5.55 (holotype).

Hypsugo lophurus—MYANMAR: Tanintharyi; Maliwun. BM(NH) 1914.12.1.6 (holotype).

Hypsugo macrotis—INDONESIA: West Sumatra; Padang. RMNH 35469–35471 (syntypes). INDONESIA: Sumatra; Riau, Japura, Indragiri. MHNG 1486.94.

Hypsugo mordax—INDONESIA: Java. ZMB 2559 (holotype).

Hypsugo petersi—INDONESIA: Buru Regency; Kayeli. BM(NH) 1897.12.6.2. MALAYSIA: Sabah; Sinsuron, Crocker Range, 1,500 m. BM(NH) 1985.908, 1985.909, 1985.910, 1985.911. PHILIPPINES: Luzon; 0.8 km N and 1.5 km E of the south peak of Mt. Data, 2,128 m. FMNH 188235, 188238. PHILIPPINES: Luzon; 0.5 km N and 0.5 km W of the peak of Mt. Amuyao, 2,530 m. FMNH 193513. PHILIPPINES: Luzon, La Laguna. MNHN 1987-356.

Hypsugo pulveratus—CHINA: Fujien; Amoy (now Xiamen). BM(NH) 1870.7.18.12 (holotype). VIETNAM: Quang Binh Province; Ke Bang. ZMMU S-167186.

Hypsugo vordermanni—INDONESIA: Borneo, Sarawak; Samunson Forest Sanctuary. RMNH 35570 (holotype).

Nyctalus leisleri—RUSSIA: Voronezh Region; Voronezhskiy State Reserve. ZMMU S-176068.

Philetor brachypterus—INDONESIA: West Sumatra; Padang. RMNH 35155 (holotype). INDONESIA: Borneo, Kalimantan, North Kalimantan; Kayan Mentarang Nature Reserve, Lalut Birai Reserve Station, 2.85N, 115.80E. ROM 102165, 102019. MALAYSIA: Johor; Endau Rompin National Park, 2.533N, 103.40E. ROM 113087.

Pipistrellus stenopterus—INDONESIA: North Sumatra; Medan. ZMMU S-103146, 103147, 103148, 103149, 103150.

Tylonycteris fulvida—MYANMAR: Schwe Gyin; valley of Sittang River. BM(NH) 1915.4.29.1, 1915.4.29.2 (syntypes).

Tylonycteris malayana—MALAYSIA: Perak; Batang Padang, Jor. BM(NH) 1947.1433 (holotype). VIETNAM: Binh Phouc Province; Bu Gia Map. ZMMU S-186637.

Tylonycteris pachypus—INDONESIA: Banten; Bantam (now Banten). RMNH 35248, 35249, 35250 (syntypes).

Tylonycteris robustula—MALAYSIA: Borneo, Sarawak; Upper Sarawak. BM(NH) 1911.1.18.8 (holotype).

APPENDIX II

Species, tissue/voucher number, locality, GenBank accession numbers, and references for sequences used in this study.

Species	Tissue/voucher #	Locality	<i>CoI</i>	<i>Cytb</i>	<i>Rag2</i>	Reference
<i>Arielulus circumdatus</i>	BNB 055	Vietnam	MF038573	MF038474	MF038336	Hassanin et al. (2018)
<i>Barbastella barbastellus</i>	HNHM 24733	Hungary	MF038569	MF038470	MF038332	Hassanin et al. (2018)
<i>Cassistrellus dimissus</i>	MHNG 1926.053	Laos	MG194430	MG194436	GU328057	Lack et al. (2010); Ruedi et al. (2018)
<i>Cassistrellus yokdonensis</i>	ROM 107765	Vietnam	HM540266	MG194435	MG194433	Francis et al. (2010); Ruedi et al. (2018)
<i>Chalinolobus neocaledonicus</i>	2000-273		MF038571	MF038472	MF038334	Hassanin et al. (2018)
<i>Eptesicus serotinus</i>	ZMMU S-183029	Russia	JF442822			Kruskop et al. (2012)
<i>Eptesicus serotinus</i>	ZMMU S-191978	Russia		GQ272579		Artyushin et al. (2009)
<i>Eptesicus serotinus</i>	MHNG 1807.065	Greece			HM561650	Roehrs et al. (2010)
<i>Falsistrellus tasmaniensis</i>	ABTC5974	Australia	MH753135	MH753138	MH753141	Görföl and Csorba (2018)
<i>Glauconycteris superba</i>	MNHN 2016-2803	DR Congo	MF038653	MF038552	MF038390	Hassanin et al. (2018)
<i>Glischropus bucephalus</i>	HNHM 2006.34.37.	Cambodia	KR612334	KR612331	MH753142	Csorba et al. (2015); Görföl and Csorba (2018)
<i>Hesperoptenus blandfordi</i>	CPV10-40		MF038582	MF038482	MF038342	Hassanin et al. (2018)
<i>Hesperoptenus tickelli</i>	CPV10-21		MF038583	MF038483	MF038343	Hassanin et al. (2018)
<i>Hypsugo cadornae</i>	HNHM 25057	Vietnam	MH753136	MH753139	MH753143	Görföl and Csorba (2018)
<i>Hypsugo dolichodon</i>	CBC02156	Cambodia	MH234219	MH234221	MH753144	Görföl et al. (2018); Görföl and Csorba (2018)
<i>Hypsugo petersi</i>	FMNH 193513	The Philip-pines	MG194431	JX570897	JX570913	Heaney et al. (2012); Ruedi et al. (2018)
<i>Hypsugo pulveratus</i>	ROM 110689	Laos	HM540657	KX429686	MH753145	Francis et al. (2010); Lim et al. (2016); Görföl and Csorba (2018)
<i>Hypsugo savii</i>	MIBZPL01295	Italy	FR856654			Galimberti et al. (2012)
<i>Hypsugo savii</i>	MHNG 1805.007	Switzerland		AJ504450		Stadelmann et al. (2004b)
<i>Hypsugo savii</i>	MHNG 1804.100	Switzerland			HM561667	Roehrs et al. (2010)
<i>Ia io</i>	VN11-0688		MF038584	JX465365	MF038344	Hassanin et al. (2018)
<i>Laephotis botswanae</i>	ECJS-11/2009		MF038572	MF038473	MF038335	Hassanin et al. (2018)
<i>Lasionycteris noctivagans</i>	MVZ 192695	United States	GU723196			Streicker et al. (2010)
<i>Lasionycteris noctivagans</i>	22Jul09-03-AHH, M37176	Unites States		KC747682		Patrick and Stevens (2014)
<i>Lasionycteris noctivagans</i>	TK24216, TTU 56255	United States			GU328065	Lack et al. (2010)
<i>Lasiurus cinereus</i>	TX6295	United States	GU722978			Streicker et al. (2010)
<i>Lasiurus cinereus</i>	TK78926	United States		KC747685	HM561638	Patrick and Stevens (2014); Roehrs et al. (2010)
<i>Mimetillus moloneyi</i>	HNHM 23243	Cameroon	MF038570	MF038471	MF038333	Hassanin et al. (2018)

APPENDIX II. CONTINUED

Species	Tissue/voucher #	Locality	<i>Col</i>	<i>Cytb</i>	<i>Rag2</i>	Reference
<i>Mirostrellus joffrei</i>	IEBR VN16-170	Vietnam	MN813969	MN813973	MN813977	This study
<i>Mirostrellus joffrei</i>	HNHM 26037	Vietnam	MN813970	MN813974	MN813978	This study
<i>Mirostrellus joffrei</i>	HNHM 26040	Vietnam	MN813971	MN813975	MN813979	This study
<i>Myotis muricola</i>	IEBR VN11-1186	Vietnam	MH137299	MH137365	MH137496	Tu et al. (2018)
<i>Neoromicia nanus</i>	ROM 100552	Cote d'Ivoire	JF444203			Eger et al. (unpublished)
<i>Neoromicia nanus</i>	ECJS_45_2009, TM 48486	Botswana		KM886076		Goodman et al. (2015)
<i>Neoromicia nanus</i>	DM 7542	South Africa			GU328062	Lack et al. (2010)
<i>Nyctalus leisleri</i>	ZMMU S-167374	Russia	JF443043			Kruskop et al. (2012)
<i>Nyctalus leisleri</i>	M1473, MHNG 1956.071	Switzerland		JX570901		Heaney et al. (2012)
<i>Nyctalus leisleri</i>	FMNH140374	Pakistan			HM561657	Roehrs et al. (2010)
<i>Nycticeinops schlieffeni</i>	UP 0775	South Africa	KF452658			McCulloch (unpublished)
<i>Nycticeinops schlieffeni</i>	IVB S657	Senegal		JX276305		Koubinova et al. (2013)
<i>Nycticeius humeralis</i>	ASNHC 12501	United States	GU723247			Streicker et al. (2010)
<i>Nycticeius humeralis</i>	LSUMZ M8901	United States		KC747697		Patrick and Stevens (2014)
<i>Nycticeius humeralis</i>	TK26380, TTU 49536	United States			GU328096	Lack et al. (2010)
<i>Parastrellus hesperus</i>	MVZ 198302	United States	GU723249			Streicker et al. (2010)
<i>Parastrellus hesperus</i>	NK32223, MSB 75640	United States		KC747698		Patrick and Stevens (2014)
<i>Parastrellus hesperus</i>	TK78703, TTU 79269	United States			GU328099	Lack et al. (2010)
<i>Perimyotis subflavus</i>	JJ107	United States	GU723254			Streicker et al. (2010)
<i>Perimyotis subflavus</i>	TK90671, TTU 80684	United States		AJ504449	GU328103	Stadelmann et al. (2004a); Lack et al. (2010)
<i>Philetor brachypterus</i>	ROM 102019	Indonesia	HM541204	KX429688		Francis et al. (2010); Lim et al. (2016)
<i>Philetor brachypterus</i>	JLS274, FMNH 180236	The Philip-pines			JX570922	Heaney et al. (2012)
<i>Pipistrellus pipistrellus</i>	ZMMU S-180542	Switzerland	JF443078			Kruskop et al. (2012)
<i>Pipistrellus pipistrellus</i>	MHNG 1807.052	Greece		AJ504443		Stadelmann et al. (2004a)
<i>Pipistrellus pipistrellus</i>	M1439, MHNG 1956.031	Switzerland			HM561662	Roehrs et al. (2010)
<i>Plecotus macrobullaris</i>	Pi08	Spain	KR134391	KR134391	GU328106	Alberdi et al. (2015); Lack et al. (2010)
<i>Scotomanes ornatus</i>	VN11-0238	Vietnam	MF038585	MF038484	MF038345	Hassanin et al. (2018)
<i>Scotophilus heathii</i>	ROM 107786		HM541926	EU750944	GU328112	Trujillo et al. (2009); Francis et al. (2010); Lack et al. (2010)

APPENDIX II. CONTINUED

Species	Tissue/voucher #	Locality	<i>Co1</i>	<i>Cytb</i>	<i>Rag2</i>	Reference
<i>Thainycteris torquatus</i>	GS 20813		MF038577	MF038478	MF038338	Hassanin et al. (2018)
<i>Tylonycteris malayana</i>	VN11-0022	Vietnam	KX496402	KX496401		Tu et al. (2017)
<i>Tylonycteris malayana</i>	M1538, MHNG 1970.041	Laos			JX570928	Heaney et al. (2012)
<i>Tylonycteris tonkinensis</i>	M1203, MHNG 1926.059	Laos	KX496442	KX496441	HM561673	Roehrs et al. (2010); Tu et al. (2017)
<i>Vespertilio murinus</i>	GTHU757, HNHM 24293	Hungary	MN813972	MN813976	MN813980	This study