



## A new genus and species of vespertilionid bat from the Indomalayan Region

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Bats belonging to the subfamily Vespertilioninae are diverse and cosmopolitan, but their systematic arrangement remains a challenge. Previous molecular surveys suggested new and unexpected relationships of some members compared to more traditional, morphology-based classifications, and revealed the existence of taxonomically undefined lineages. We describe here a new genus and species corresponding to an enigmatic lineage that was previously identified within the genus *Eptesicus* in the Indomalayan Region. Phylogenetic reconstructions based on mitochondrial and nuclear genes relate the new taxon to *Tylonycteris* and *Philetor*, and show that specimens associated with this new genus represent 2 genetically distinct species. Although little is known about their ecology, locations of capture and wing morphology suggest that members of this new genus are tree-dwelling, open-space aerial insect predators. The new species has only been documented from Yok Don National Park in Vietnam, so its conservation status is uncertain until more surveying methods target the bat fauna of the dipterocarp forest in Southeast Asia.

Key words: eptesicoid bats, phylogeny, systematics, taxonomy, Vespertilionidae

Bats of the family Vespertilionidae represent a large radiation containing over 400 species. Among mammals, this family is 2nd only to the rodent family Muridae in terms of diversity. These rather nondescript bats colonized a wide variety of habitats and are present virtually across the world, excluding the polar regions. Their external morphology is characterized by an absence of derived appendages, such as a nose leaf, although special attributes such as greatly enlarged ears or the presence of adhesive pads near wrists or ankles are found in a few, independent lineages. Hence, most of the traditional subdivisions of vespertilionid bats were based chiefly on skull and dental characters (Tate 1942; Koopman 1994).

When the 1st systematic surveys of this family were performed with novel characters, such as karyotypes (Heller and Volleth 1984; Volleth and Heller 1994; Volleth et al. 2006) and bacular morphology (Hill and Harrison 1987), it became obvious that many parallelisms or convergences produced similar external or dental phenotypes that evolved independently, and hence the phylogenetic hypotheses based on such characteristics would lead to unnatural classifications. Within the family of vesper bats, the most diverse and taxonomically perhaps the

most challenging subfamily is the Vespertilioninae. The following 2 species-rich groups illustrate this systematic difficulty: the pipistrelloid and the eptesicoid bats were traditionally separated by the presence or absence, respectively, of a 2nd upper premolar (Tate 1942). Karyological surveys (Heller and Volleth 1984; Volleth and Heller 1994; Kearney et al. 2002; Koubinova et al. 2013) showed that these bats indeed represent 2 major evolutionary lineages, one characterized by high and constant chromosome number (fundamental number [FN] = 50), whereas the other had a reduced and more variable set of chromosomes (FN = 44 or less), respectively; however, none of these main karyological lineages matched the groups defined by dental characters. Hill and Harrison (1987) reached similar conclusions by examining bacular traits of vespertilionids, and suggested subdividing the species-rich genera *Eptesicus* and *Pipistrellus* into several subgenera.

The use of molecular characters further confirmed the paraphyletic nature of these genera (e.g., Hooper and Van Den Bussche 2003), and highlighted the necessity to raise most of the proposed subgenera to full generic rank to better reflect the phylogenetic groupings. Despite this progress toward a natural

classification of vespertilionid bats and even with denser taxon and character samplings (Lack and Van Den Bussche 2010; Roehrs et al. 2010; Koubinova et al. 2013), the relationships of several lineages within the Vespertilioninae could not be firmly established. Notably, species included in the informally designated “hypsugine group” (Roehrs et al. 2010) appeared within the tribe Vespertilionini, but the tribe itself was poorly resolved in large phylogenies (e.g., Amador et al. 2016).

In a large molecular survey aimed primarily to better understand the evolution of the Myotinae (Lack et al. 2010), one of the sequenced specimens was a bat originating from Laos and morphologically identified as *Eptesicus dimissus* Thomas, 1916. This species is apparently extremely rare and was previously known by the type caught in peninsular Thailand (Robinson and Kloss 1915), and by a series of 8 individuals captured in or near the Royal Chitwan National Park in Nepal (Myers et al. 2000b). In all molecular phylogenies, the new Lao specimen was consistently placed away from all other assayed *Eptesicus*, but clustered together with morphologically highly specialized bats such as *Tylonycteris* or *Hypsugo* (Lack et al. 2010; Koubinova et al. 2013). In another large survey of molecular diversity of Southeast Asian bats based on a mitochondrial barcode gene (Francis et al. 2010), a lineage associated with an unknown *Eptesicus* (called *Eptesicus* sp. A JLE-2010) also appeared distantly related to other congeners. Based on a morphological and molecular re-examination of all available specimens associated with these enigmatic lineages, we propose a new classification and taxonomic treatment for these bats in the Vespertilionidae.

## MATERIALS AND METHODS

**DNA analyses.**—Tissue suitable for DNA sequencing was only available from the more recent Laos and Vietnam bats, the older known specimens from Thailand and Nepal associated with *E. dimissus* were fixed in formalin. Total DNA was extracted and purified with the Blood and Tissue Kit (Qiagen AG, Hombrechtikon, Switzerland) according to manufacturer’s manual and eluted in a final volume of 200  $\mu$ l TE buffer. Two mitochondrial genes, cytochrome *b* (abbreviated hereafter *Cytb*) and cytochrome *c* oxidase subunit 1 (*CoI*), and 1 nuclear gene, recombination-activating gene exon 2 (*Rag2*), were amplified and sequenced following the strategy of Stadelmann et al. (2007). The primer pairs used to amplify the complete *Cytb*, MOLCYTF (Ibáñez et al. 2006) and H15915 (Irwin et al. 1991), target a large fragment of DNA (about 1,200 bp) that could not be obtained from the Laos specimen, probably because of some tissue degradation. For this specimen, we therefore amplified the *Cytb* as 2 smaller, overlapping fragments using MOLCYTF and H14149 (Kocher et al. 1989), and a newly designed one L15162\_DIM (5'-GTTATGTATTRCCATGAGGRCAAATRTC-3') with H15915. The *CoI* gene was amplified with the primers UTyr and C1L705 following Hassanin et al. (2012) or with the M13-tailed vertebrate primer cocktails following Francis et al. (2010). We also included in this sequencing process a related

taxon, *Falsistrellus petersi*, which was sequenced previously for *Cytb* and *Rag2* genes (Heaney et al. 2012), but not for the *CoI*. Amplicons were purified and sent for sequencing to a commercial lab (Macrogen Inc., Amsterdam, The Netherlands) or sequenced in the Canadian Centre for DNA Barcoding at the University of Guelph and the Laboratory of Molecular Systematics at the Royal Ontario Museum. Fragments were sequenced in both directions with the same PCR primers. The resulting chromatograms were checked for double peaks or stop codons, which in mitochondrial genes would signal the presence of pseudogenes. Double peaks in the *Rag2* sequences were interpreted as heterozygous nucleotide positions and signaled as such with IUPAC ambiguity codes. Chromatograms were visualized, aligned, and assembled with Sequencher 4.1 (Gene Codes Corp., Ann Arbor, Michigan).

**Phylogenetic reconstruction.**—As several molecular phylogenies of Vespertilionidae including the *dimissus* lineage and based on intensive taxon and character sampling have already been produced (e.g., Roehrs et al. 2010; Koubinova et al. 2013), our intent here was not to replicate these comprehensive analyses. Rather, we focused on the tribes Eptesicini-Nycticeini, Vespertilionini, and Pipistrellini containing all representatives of *Eptesicus* analyzed so far (Juste et al. 2013), and species related to the *dimissus* lineage. The list of taxa and source of homologous gene sequences used in our alignments are available in Appendix 1.

We performed phylogenetic reconstructions for the 3 genes separately and in a combined matrix and analyzed them with a Bayesian inference (BI) method and under the maximum likelihood (ML) criterion. Two species of *Scotophilus* were used as outgroups of the Vespertilioninae in all reconstructions. BI and ML analyses were realized with MrBayes v3.2.1 (Ronquist et al. 2012) and raxmlGUI v1.5 (Silvestro and Michalak 2012; Stamatakis 2014), respectively. Reliability of nodes in ML analyses was assessed by 1,000 rapid bootstraps with RAxML (Stamatakis et al. 2008). All analyses were performed using a fully partitioned scheme where each gene and codon position was allowed to have specific model parameters. The General Time Reversible (GTR) model with “Gamma” and “Invariant Sites” was used in each partition, following results from PartitionFinder 2 (Guindon et al. 2010; Lanfear et al. 2012, 2017).

To obtain BI trees, MrBayes was run for 1 million generations and sampled every 1,000. The 1st 10% of generations were discarded as burn-in. Posterior probabilities were subsequently computed from the consensus of the remaining sampled trees. Two parallel runs were performed on each data set and results combined. Tracer v1.5 (Rambaut and Drummond 2009) was used to ensure that the likelihood scores had stabilized and that effective sample sizes for the estimated parameters and posterior probability were higher than 200.

To assess level of genetic differentiation between lineages, and for comparative purpose with previous surveys, we used the Kimura 2-parameter model (K2P—Kimura 1980) to estimate pairwise genetic distances, as implemented in the program MEGA7 (Kumar et al. 2016).

*Morphological comparisons.*—Eight external measurements were taken from the specimen label or measured on the preserved specimens with digital calipers (to the nearest 0.1 mm), whereas 17 craniodental characters were measured by one of us (GC) to the nearest 0.01 mm. The characters were defined in Csorba et al. (2014) and Görföl et al. (2014) and included: forearm length (FA); tail length (TL); head and body length (HB); hindfoot length including claws (HF); tibia length (TIB); ear length (EAR); tragus length (TRA); W (body mass, expressed in grams); greatest length of skull including incisors (GTL) and excluding incisors (STOTL); condylo-canine length (CCL); width across the upper canines (CCW); width across the upper molars (M3M3W); interorbital width (IOW); mastoid width (MAW); rostral width between the lachrymal openings (RW); braincase width (BCW); braincase height (BCH); maxillary toothrow length (CM3L); upper canine–premolar length (CP4L); mandible length, without incisors (ML); length of anteorbital bridge (AOB); mandibular toothrow length (cm3L); lower canine–premolar length (cp4L); and least height of the coronoid process (CPH). The designation of specific parts of the skull or the external morphology generally follows the nomenclature and definitions used by Tate (1942). Capture and handling of the newly obtained specimens conform to the principles and guidelines of the American Society of Mammalogists (Sikes et al. 2016).

As the sparse material available for the *dimissus* lineage consists of partially damaged skulls or immature individuals, we did not perform statistical morphometric analyses. Instead we relied on direct comparisons of specimens housed in various collections, the acronyms of which are AMNH: American Museum of Natural History, New York, United States; BM(NH): Natural History Museum (formerly British Museum (Natural History)), London, United Kingdom; FMNH: the Field Museum of Natural History, Chicago, United States; HNHM: Hungarian Natural History Museum, Budapest, Hungary; MHNG: Muséum d'histoire naturelle de Genève, Geneva, Switzerland; MNHN: Muséum national d'histoire naturelle, Paris, France; RMNH: Naturalis (Nationaal Natuurhistorisch Museum; formerly Rijksmuseum van Natuurlijke Historie), Leiden, The Netherlands; ROM: Royal Ontario Museum, Toronto, Canada; UMMZ: University of Michigan Museum of Zoology, Ann Arbor, United States; IEBR: Institute of Ecology and Biological Resources, Hanoi, Vietnam; ZSI: Zoological Survey of India, North Eastern Regional Centre, Shillong, India.

*Material for comparisons.*—The following comparative material was used. *Arielulus torquatus*: HNHM 2004.19.29, adult female, Taiwan. “*Eptesicus*” sp.: ROM 107765, subadult female with slightly damaged skull, Yok Don National Park, central Vietnam; ROM 107751, a juvenile male with damaged skull, captured in the same place in Vietnam. “*Eptesicus*” *dimissus*: BM(NH) 16.4.21.1 (type), subadult female with partly damaged skull, Tai Rom Yen National Park, southern Thailand (Robinson and Kloss 1915; Thomas 1916); UMMZ 17218, adult female with intact skull, the Royal Chitwan National Park, Nepal (Myers et al. 2000b); UMMZ 172223,

adult male with intact skull and baculum prepared, the Royal Chitwan National Park, Nepal (Myers et al. 2000b); MHNG 1926.053, adult male with intact skull and baculum prepared, Ban Naten, in the Nam Lan Conservation Area, Phongsaly, northern Laos (Fuchs et al. 2007). *Eptesicus pachyomus andersoni*: IEBR VN11-0076, adult male, Vietnam. *Eptesicus pachyomus horikawai*: HNHM 2004.19.27, adult female, Taiwan; HNHM 2004.19.28, adult male, Taiwan. *Eptesicus pachyomus pallens*: HNHM 98.3.2, adult female, Vietnam; HNHM 25861, adult male, China. *Eptesicus serotinus serotinus*: HNHM 75.90.1, adult female, Hungary; MHNG 1807.065, adult male, Greece. *Falsistrellus mackenziei*: AMNH 160344, adult male, Australia. *Falsistrellus petersi*: AMNH 206748, adult male, Philippines. *Glischropus tylopus*: MHNG 1970.063, adult female, Peninsular Malaysia. *Hesperoptenus blanfordi*: HNHM 2005.82.51, adult male, Laos; MHNG 1970.053, adult female, Peninsular Malaysia. *Hesperoptenus tickelli*: HNHM 2005.81.25, adult male, Cambodia. *Hypsugo cadornae*: MHNG 1926.050, adult female, northern Laos. *Hypsugo dolichodon*: ROM 110459 (holotype), adult female, Laos. *Hypsugo joffrei*: ZSI V/M/ERS/292, adult male, India (Saikia et al. 2017). *Neoromicia capensis*: HNHM 76.162.1, adult male, Zambia. *Nyctalus leisleri*: MHNG 1956.071, adult female, France. *Nyctalus noctula*: MHNG 1811.056, adult female, Switzerland. *Nyctophilus timoriensis*: MNHN 2004.1268, adult female, Australia. *Philetor brachypterus*: RMNH 35155 (holotype), adult male, Sumatra, Indonesia; BM(NH) 1985.914, adult male, Borneo, Malaysia. *Rhynptesicus nasutus*: HNHM 25491, adult male, United Arab Emirates. *Scotoanax rueppelii*: AMNH 183376, adult male, Australia. *Scotoecus hirundo*: MNHN 2004-1273, adult female, Kenya. *Scotoecus pallidus*: AMNH 54420, unknown sex and date, India. *Scotomanes ornatus*: HNHM 86.9.1, adult male, Vietnam; MHNG 1926.051, adult male, Laos. *Scotophilus heathii*: MHNG 1926.052, adult male, Laos. *Scotophilus kuhlii*: HNHM 92.123.6, adult male, India. *Scotorepens sanborni*: AMNH 108709, adult female, Papua New Guinea. *Tylonycteris fulvida*: MHNG 1926.055, adult male, Laos. *Tylonycteris pachypus*: RMNH 35249 (syntype), Java, Indonesia. *Tylonycteris tonkinensis*: MHNG 1926.059, adult male, Laos (Tu et al. 2017). *Vespadelus pumilus*: AMNH 107795, adult female, Australia. *Vespertilio murinus*: HNHM 2857.27, adult male, Slovakia; MHNG 1957.087, adult female, Switzerland.

## RESULTS

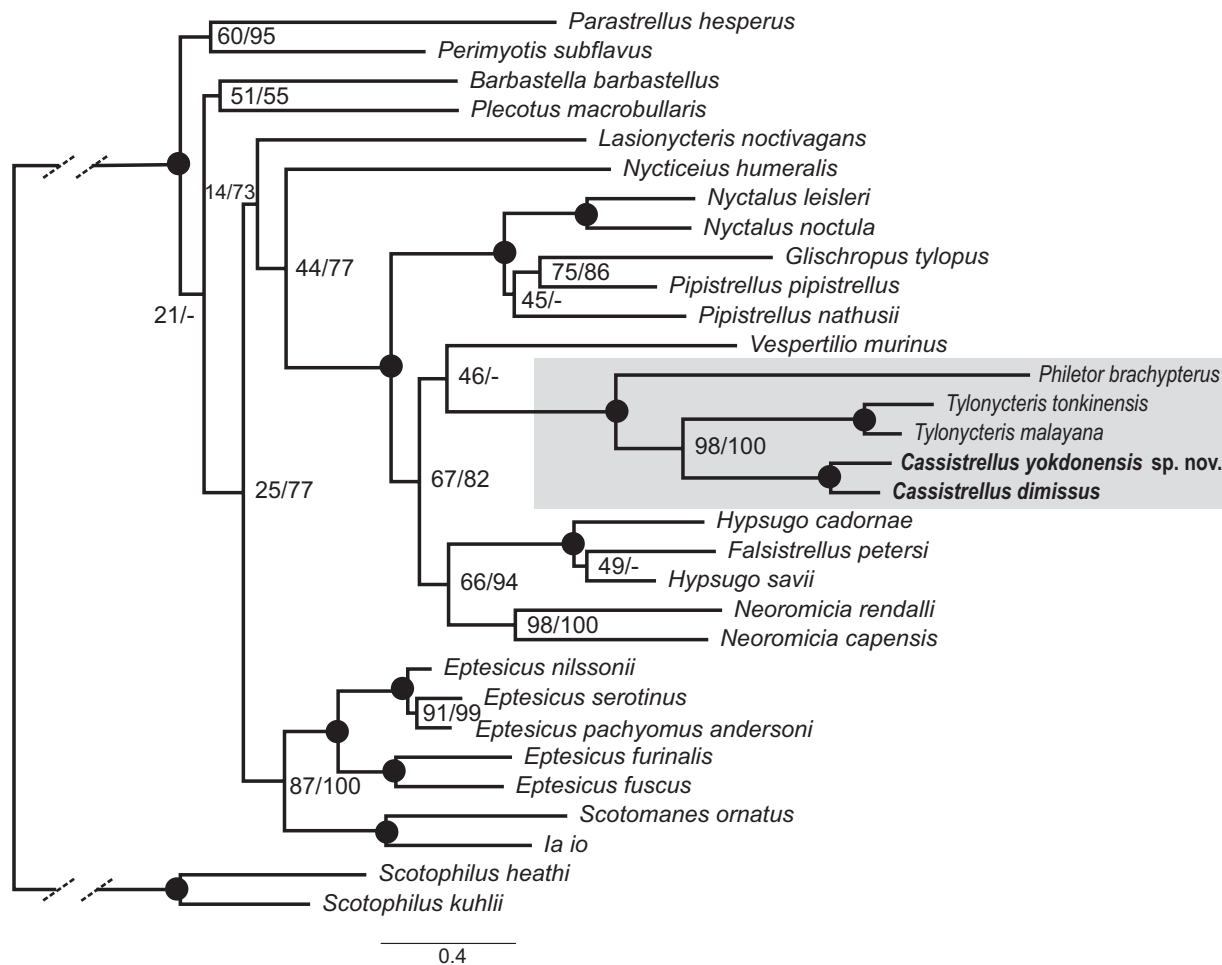
*DNA sequences.*—DNA sequences newly obtained for the *dimissus* lineage include the complete *Cytb* (1,140 bp) of the two Vietnamese specimens ROM 107751 and 107765 (deposited under GenBank number MG194434 and MG194435), but only part (829 bp) of this mitochondrial gene for the Lao specimen MHNG 1926.053 (MG194436). The latter and *Falsistrellus petersi* FMNH 193513 were also sequenced for 674 bp of the *CoI* gene (MG194430 and MG194431, respectively). We obtained *Rag2* sequences (1,233 bp) for the 2 Vietnamese samples of the *dimissus* lineage (MG194432 and

MG194433). Other sequences and associated GenBank numbers for the same individuals obtained in previous projects (Francis et al. 2010; Lack et al. 2010; Heaney et al. 2012) are listed in Appendix 1.

For the *Cytb* gene, both Vietnamese specimens had the same haplotype and differed from the Lao *E. dimissus* by 9.9% K2P distance. For the *Co1* fragment, the ROM 107765 specimen also differed by a similar genetic distance (10.4%). For the *Rag2* fragment, the 2 ROM bats differed from each other by a single transition mutation (0.1%), and by 7 (= 0.6%) from the MHNG *E. dimissus*. Blast comparisons in GenBank (as of June 2017) lead to distances that are several times larger, the most similar ones being sequences of *Tylonycteris* spp. at about 20% for the mitochondrial and about 4% for the nuclear genes. Interestingly, when the *Rag2* sequences of the *dimissus* lineage are aligned with those of other bats, they share a rare codon insertion (CAA; located near residue position 1077 in a homologous human sequence of *Rag2*) that is only found in *Tylonycteris*, *Philetor*, and *Pipistrellus*. All other bats sequenced lack this codon in their *Rag2* genome. For all subsequent analyses, this inserted codon was omitted from phylogenetic reconstructions,

as each of these 3 component nucleotides cannot be considered independent characters.

*Phylogeny.*—All phylogenetic reconstructions, whether based on the 3 genes taken separately (not shown) or in combination (Fig. 1), strongly supported (98% bootstrap and 100% posterior probability) sister-group relationships between representatives of the *dimissus* lineage and *Tylonycteris*, with *Philetor* sister to this clade. None of our reconstructions placed *E. dimissus* within the strongly supported clade formed by all remaining *Eptesicus* species (Fig. 1), nor was it associated with the divergent genus *Rhyneptesicus* (based on the mitochondrial genes, not shown), which was long considered belonging to *Eptesicus* (but see Juste et al. 2013). Although these results corroborate previous phylogenetic reconstructions, we cannot infer the sister group of this clade within the Vespertilioninae due to uncertainties associated with nodes deeper in the tree. It appears most closely related to *Vespertilio* in the combined gene analysis inferred with RAxML (albeit with very weak support; Fig. 1), but not in the Bayesian reconstructions (57% posterior probability support for a sister-group relationship with the hypsugine group



**Fig. 1.**—Maximum likelihood (ML) phylogeny of selected Vespertilioninae bats based on a combined alignment of 2 mitochondrial and 1 nuclear gene (2,161 bp in total). Numbers near nodes indicate branch support (left, percent ML bootstrap, right, posterior probability), while solid circles represent nodes recovered in >98% of both resampling methods. The gray box highlights the strongly supported clade comprising species of *Cassistrellus* gen. nov., *Tylonycteris*, and *Philetor*.

sensu Roehrs et al. 2010). Clearly, all molecular reconstructions indicate that the *dimissus* lineage does not belong in *Eptesicus*. In order to reflect its divergent evolutionary history among the Vespertilioninae, and because no specific generic name was published in earlier reports dealing with this taxon (e.g., Tate 1942; Hill and Harrison 1987; Simmons 2005), we herewith describe it as a new genus.

*Cassistrellus* gen. nov.

*Type species.*—*Eptesicus dimissus* Thomas, 1916

*Description.*—Species of *Cassistrellus* are medium-sized vespertilionids (FA 39–47 mm; body mass 12–17 g) characterized externally by short, chestnut-brown pelage that is paler on the ventral parts, by narrow wings with short and pointed tips, and an especially broad muzzle (Fig. 2). Wing membranes are attached to the middle or distal parts of the metatarsus. The tail is mostly included in the uropatagium and extends by 2–3 mm beyond its posterior margin. The calcar extends less than halfway to the tail and may have a small lobe near the ankle. The skull is robust and angular in profile making an almost straight line between the rostrum and the occipital region. It is characterized by well-developed sagittal and lambdoid crests, which meet near the top of the skull to form an occipital helmet. On its ventral surface, the skull has a pair of deep and well-delimited basisphenoid pits located between the cochleae (Fig. 3). Laterally, the lachrymal region has prominent preorbital processes, but the supraoccipital ridges are weak and barely visible. The dental formula is  $\frac{2113}{3123} = 32$  teeth, with the upper canines possessing a distinct secondary cusp along the rear edge (Fig. 3).

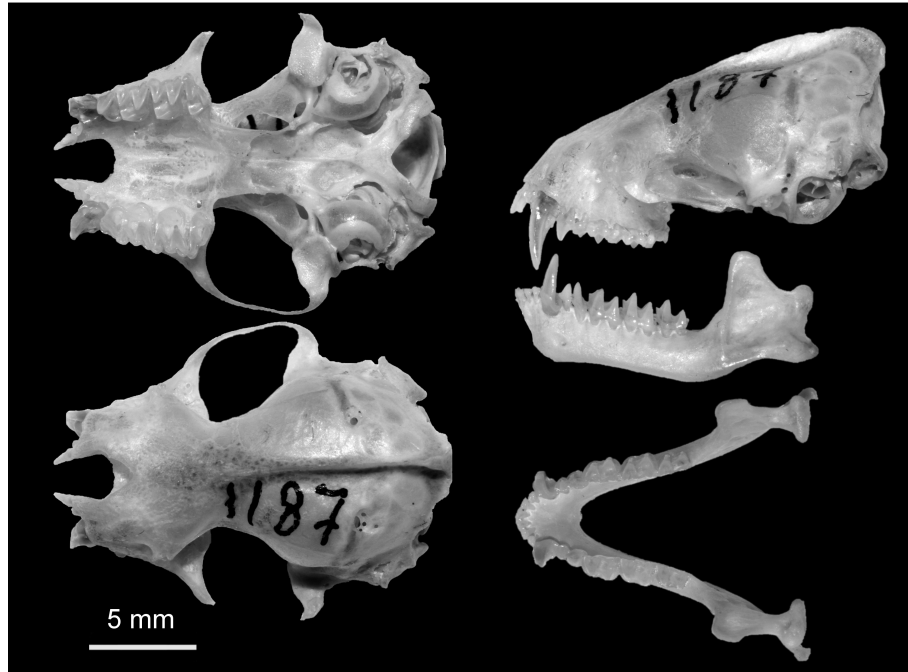
*Etymology.*—The name *Cassistrellus* derives from the Latin noun “*cassis*”, which means wearer of a helmet, in reference to the shape of the hind parts of the skull. The suggested English vernacular name is helmeted bat.

*Diagnosis and comparisons.*—Because *Cassistrellus dimissus* was associated traditionally with species in the *Eptesicus serotinus* group (Tate 1942; Hill and Harrison 1987; Simmons 2005), we compared it to members of that group, although externally the new genus resembles *Nyctalus*, *Philetor*, or even the smaller *Hypsugo joffrei* (see illustration in Saikia et al. 2017), owing to its rather uniform chestnut-brown coloration (Fig. 2), short ears and narrow, pointed wings. *Eptesicus* species have much longer and wider wings and although their fur color may vary from dark brown to pale sandy, they never show a chestnut tinge, they appear shiny due to light-tipped hairs of dorsal fur, and their ears are more elongated. Furthermore, the fur of *Cassistrellus* is short (about 3 mm mid-dorsum) and sparse, while it is denser and longer (> 5 mm) in *Eptesicus*, including all Asian species such as *E. tatei*, *E. pachyotis*, or *E. serotinus* (Dobson 1871). Hairs of ventral and dorsal fur in *Cassistrellus* are paler toward the base, while they become invariably darker in *Eptesicus*. These differences in wing shape, coloration, and fur characteristics were noted by Thomas (1916) when he distinguished *E. dimissus* from *E. pachyotis* and added that the latter had the wing insertion at the base of the toe, whereas it inserts on the metatarsus in *E. dimissus* (but see variation of this character hereafter). External measurements of *Cassistrellus* (Table 1) indicate that they are medium-sized vespertilionids.

Ears of *Cassistrellus* are rather small (about 16 mm), triangular, fleshy, and do not extend much beyond the top of the head (Fig. 2), much like those in *Nyctalus* and *Philetor*. Ears are more elongated and proportionally longer in species of the *serotinus* group. Like in *Nyctalus*, the posterior margin of the pinna folds back and extends round nearly to the corners of the mouth (Fig. 2), but is not exceptionally fleshy and thick, as in *Eptesicus pachyotis* (Tate 1942; Hill and Harrison 1987; Myers et al. 2000b). The tragus of *Cassistrellus* is small, rounded-off and curved inwards, as in *Philetor* and *H. joffrei*, but unlike



Fig. 2.—Portrait of a live adult male *Cassistrellus dimissus* captured near the Royal Chitwan National Park in Nepal in March 1990. This specimen was collected as part of the series of vouchers described by Myers et al. (2000b) and conserved at the UMMZ (photo courtesy of Phil Myers).



**Fig. 3.**—Dorsal, ventral, and lateral views of the skull and mandible of a male *Cassistrellus dimissus* from Laos (MHNG 1926.053). Notice the deep basisphenoid pits between tympanic bullae, long, cuspidate upper canines, strong lambdoidal and occipital crests, and prominent preorbital processes that are typical morphological features of *Cassistrellus* gen. nov.

**Table 1.**—External and craniodental measurements of the specimens associated with *Cassistrellus* gen. nov. Measurements are given in mm, except for body mass, which is given in g; abbreviations and acronyms of museums are defined in the text. As the specimen ROM 107765 is a juvenile, volant individual with incompletely fused epiphyses, measurements are given in parentheses as they may not correspond to normal adult conditions.

Museum	BM(NH)	UMMZ	UMMZ	MHNG	ROM	ROM
No.	16.4.21.1 (type)	172218	172223	1926.053	107751 (holotype)	107765 (paratype)
Locality	Thailand	Nepal	Nepal	Laos	Vietnam	Vietnam
Species	<i>dimissus</i>	<i>dimissus</i>	<i>dimissus</i>	<i>dimissus</i>	<i>yokdonensis</i> sp. nov	<i>yokdonensis</i> sp. nov
Sex	F	F	M	M	M	F
Age	Subadult	Adult	Adult	Adult	Subadult	Juvenile
FA	41.5	38.9	39.4	41.8	47.5	(43.0)
TL	41			40	52	(46)
HB	59			63	66	(61)
HF	10.0	8.8	8.9	10.0	12.0	(12.0)
TIB	15.0	14.5	15.4	16.2	15.2	(14.6)
EAR	16.0			15.4	16.0	(14.0)
TRA				6.0	7.0	(7.0)
W				15	15	(12)
GTL	17.4	16.6	17.0	18.6	17.9	(17.1)
STOTL		15.8	16.1	17.6	16.9	(16.5)
CCL	15.8	14.6	15.3	16.5	16.5	(15.7)
CCW		5.6	5.9	6.4	6.2	
M3M3W		7.6	7.7	8.4	8.2	
IOW		4.6	4.8	4.8	5.0	(5.0)
MAW	9.6	9.5	9.9	10.5	10.1	
RW		6.70	7.11	8.07	7.29	
BCW	8.6	8.0	8.0	8.8	8.8	
BCH		6.8	7.1	7.1	6.5	
CM3L	6.0	5.8	6.0	6.4	6.6	(6.3)
CP4L	2.5	2.4	2.4	2.6	2.6	(2.5)
ML	12.8	11.9	12.2	13.7	13.3	(13.1)
AOB	0.66	0.53	0.58	0.83	0.34	(0.42)
cm3L	6.73	6.29	6.53	7.02	7.05	(6.81)
cp4L		2.24	2.33	2.60	2.29	(2.32)
CPH	4.7	4.4	4.4	5.0	4.9	

species of the *serotinus* group, where the tragus is more elongated and nearly of equal width over most of its height.

The muzzle of *Cassistrellus* is particularly short and wide due to the inflated facial glands (Fig. 2), but is more long and slender in the *serotinus* group.

Bare parts of skin of *Cassistrellus* are pinkish brown (Fig. 2), not as dark as in most *Eptesicus*. In this respect, *E. pachyomus* is an exception as it has lighter colored face and ears than other congeners (Juste et al. 2013). Wing membranes are dark brown. Thumbs are short and stout, with strong claws, as also seen in the relatively small feet (about 8–12 mm, including claws).

Genitalia in *Cassistrellus* are simple, including the male apparatus, which is only slightly swollen near the glans penis. This is unlike *Philetor*, which has elaborate penial and vaginal structures (Tate 1942; Heller and Volleth 1989). The baculum is tiny (about  $1.0 \times 0.7$  mm) and triangular in outline (Myers et al. 2000b) much like those of the *serotinus* group (Hill and Harrison 1987), but the ventral parts have 2 lateral wings that are unseen in *Eptesicus*. Morphologically, the baculum has no similarities to either *Hypsugo* or *Philetor*, as noted by Hill and Harrison (1987).

The skull of *Cassistrellus* is robust (GTL 16–18 mm), relatively flat in profile and with a moderately inflated braincase (Fig. 3). The sagittal and lambdoid crests are well developed, at least in fully adult specimens, and coalesce to form a distinctive occipital helmet. Some large *Eptesicus* or *Scotophilus* species have a similar structure (Tate 1942; Hill and Harrison 1987). Frontally, the sagittal crest fades into ill-defined supraorbital ridges. The rostrum is relatively short and broad. The bulbous part of the lachrymal region has no frontal depression (as seen in *Vespertilio*), but bears prominent supraorbital tubercles (Fig. 3). These tubercles are also conspicuous in *Tylonycteris*, *Philetor*, and *H. joffrei*, but are completely lacking in *Eptesicus*. The tympanic bullae are relatively small, as in *Eptesicus*, and not covering entirely the cochleae.

The most distinctive character of the skull of *Cassistrellus*, and one which was the basis for creating a separate group for *E. dimissus* (Tate 1942) is the presence of deep, well-defined basisphenoid pits (also called basal pits) lying between the cochleae (Fig. 3). These pits are absent or shallow and ill-delimited posteriorly in *Eptesicus*, but well developed in genera such as *Nyctalus*, *Hesperoptenus*, and *Hypsugo* (Tate 1942).

The dentition of *Cassistrellus* is weaker and more delicate than in *Eptesicus* species of similar size. The canines are especially long and slender, whereas they are thick and robust in the latter genus. The upper toothrow (CM3L 6–7 mm) consists of 1 canine, a single premolar, and 3 molars. The lower toothrow has 1 canine, 2 premolars, and 3 molars, the latter being all myotodont (as in *Eptesicus*, *Philetor*, and *Hypsugo*), not nyctalodont as in pipistrelloid genera such as *Nyctalus* and *Pipistrellus* (Menu and Sigé 1971). The reduced dental formula with 2 upper incisors and a single upper premolar differentiate *Cassistrellus* from other vespertilionids that possess fewer incisors (e.g., *Scotophilus* and *Scotoecus*), or more upper premolars on each side (e.g., *Scotozous*, *Hypsugo*, *Nyctalus*, *Falsistrellus*, *Vespadelus*, and *Myotis*). The same dental formula is found

in *Philetor*, *Hesperoptenus* (see review in Hill and Harrison 1987), and *Eptesicus*. As in the latter genus, the inner upper incisor (I2) is large and with 2 cusps of subequal height. The 2nd, outer incisor (I3) is much reduced, reaching slightly above the cingulum of the inner one. In crown area, I3 is notably smaller than I2. I3 has 1 main cusp with 2 indistinct ones emerging posteriorly.

The upper canine of *Cassistrellus* is long and triangular in cross section and bears a notable secondary cusp (Fig. 3) on the posterior ridge. As noted by Tate (1942), such secondary cusps are never found in *Eptesicus*, but occasionally can be well developed in a few other taxa such as some *Pipistrellus* and *Hypsugo* species and in *Philetor*.

The single upper premolar of *Cassistrellus* is rather large and tightly compressed between the adjacent teeth, and subrectangular in occlusal view. It is clearly more robust and triangular in species of the *serotinus* group. The 1st 2 molars are similar in size and crown area and, albeit weaker, do not differ notably from those of *Eptesicus*. The 3rd upper molar is about half the size of other molars in crown area, with a parastyle area slightly more developed than in *Eptesicus*. In this respect, it is again more similar to the molar shape of *H. joffrei*, which also bears relatively large 3rd molars.

As noted by Myers et al. (2000b), the lower jaw in occlusal view is broader and more rounded frontally (Fig. 3), whereas it is more pointed, with convergent dentaries in *Eptesicus*, producing a more crowded row of incisors than in *Cassistrellus*. The 3 lower incisors are of comparable size and bear 3 main cusps each along the frontal ridge. The 1st incisor is spatulate in shape, whereas the 2nd and 3rd have a secondary cusp on the lingual side, making them more squarish in occlusal view. In side view (Fig. 3), the particularly long and slender lower canine is about twice as high as the premolars and has a well-developed cingulum. This tooth is relatively shorter and more robust in the *serotinus* group, including *E. pachyotis* (Lekagul and McNeely 1977). The 2 small lower premolars are nearly of the same height, the first consistently shorter than the second; in crown area the 1st premolar is about 2/3 the size of the 2nd. The 2nd lower premolar is much larger in *Eptesicus*, and the relative sizes of premolars are more disparate in that genus. The 1st 2 molars are large and of comparable size, the 3rd being only slightly smaller. This unreduced condition of the 3rd lower molar in *Cassistrellus* (Fig. 3) is a distinguishing character, as the m3 trigonid is particularly reduced in the *serotinus* group (Tate 1942).

*Geographic distribution.*—The type specimen of *C. dimissus* was collected by H. C. Robinson and E. Seimund in Kao Nawng, Bandon (currently within Tai Rom Yen National Park in Surat Thani province of Thailand) at 1,400 feet (= 436 m a.s.l.), in June 1913 (Robinson and Kloss 1915). However, the altitude associated with this specimen was reported by Thomas (1916) as 3,500 feet (= 1,067 m a.s.l.), which would correspond to near the summit of the Khao Nong mountain, where the collectors did not capture bats. As all known localities of *Cassistrellus* are located in the lowlands at elevation between 190 and 674 m a.s.l., these bats should be indeed regarded as

lowland dwellers. The vast area covered by the few scattered records of *Cassistrellus* suggests that it should be widely distributed from the Isthmus of Kra into mainland Southeast Asia and the foothills of the Himalaya, i.e., across most of the Indo-Burma biodiversity hotspot (Myers et al. 2000a). All capture sites were situated in hilly terrain with mixed deciduous or dipterocarp forests traversed by large rivers.

**Phylogenetic relationships.**—Mitochondrial and nuclear sequences suggest that *Cassistrellus* is closely related to *Tylonycteris* (Fig. 1) within the Vespertilioninae (Lack et al. 2010; Koubinova et al. 2013). However, the relatively long branches (and hence large genetic distances) leading to these terminal taxa suggest that these genera had a long independent evolutionary history. Morphologically, the highly derived characteristics of the bamboo bats (e.g., presence of adhesive pads, flattened skull, and extremely small size; see Tate 1942) probably reflect this long independent history. Based on the fossil-calibrated chronograms of Lack and Van Den Bussche (2010), the split between those 2 genera occurred about 12 Ma. Species of true *Eptesicus* appear in a distinct group that diverged at least 25 Ma from a common ancestor with the latter.

In the absence of genetic data and although craniodental measurements of the Lao specimen appear larger (Table 1) than the 2 specimens measured from Nepal, they share all typical morphological features of *Cassistrellus*, including baculum shape. All the above specimens also agreed well morphologically with the type of *C. dimissus* from Thailand (Fig. 4) and therefore are considered conspecific. The significant genetic differences (about 10% K2P for the *Cytb* or *Co1* genes) estimated between the Lao (MHNG 1926.053) and Vietnamese (ROM 107751 and ROM 107765) specimens fall well above the distance usually observed among conspecific bats, but within the range of sister species (Baker and Bradley 2006). As the latter specimens also differ on several morphological aspects from typical *C. dimissus*, we conclude that the 2 ROM specimens represent another, unknown species of *Cassistrellus* which we describe herein.

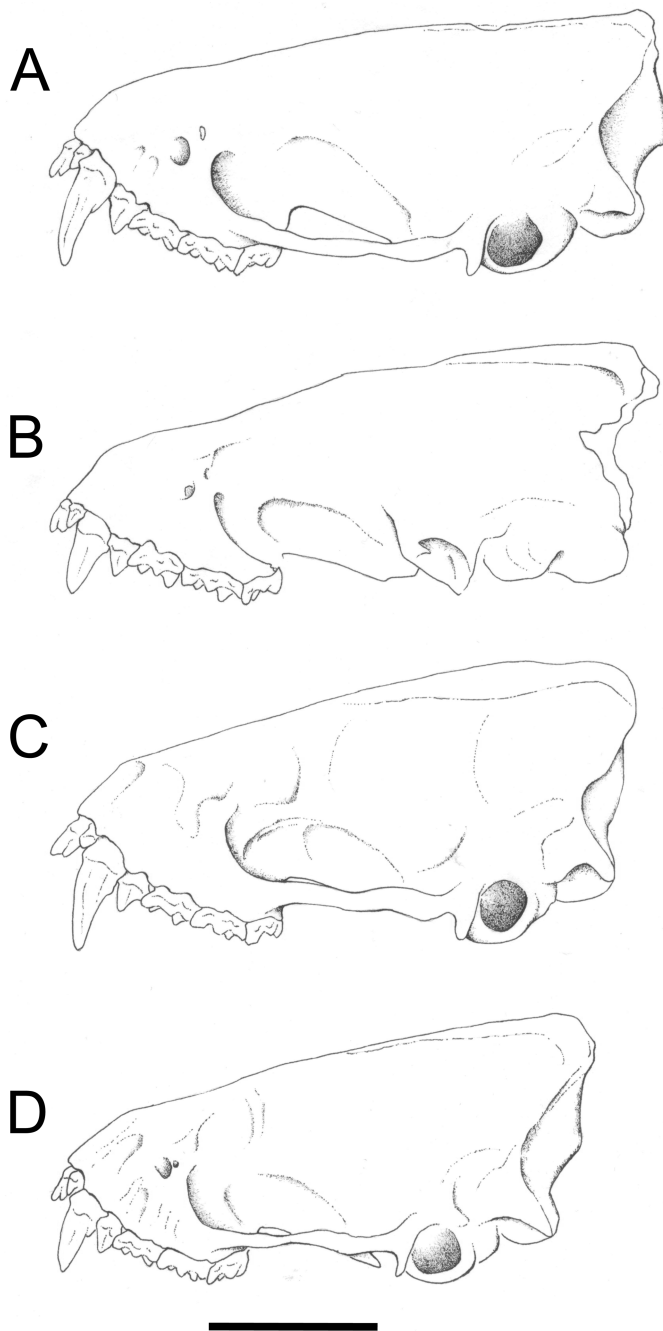
*Cassistrellus yokdonensis* sp. nov.  
Yok Don helmeted bat

*Eptesicus* sp. A JLE-2010: Francis et al., 2010

**Holotype.**—Male ROM 107751 (field number 42734) collected on 6 June 1997 by B. K. Lim and M. Theberge. Preserved as a skin, skull, and partial skeleton. Epiphyses almost completely fused, indicating that this bat was a subadult.

**Type locality.**—Vietnam: Dak Lak province; Yok Don National Park, Dak Ken River (tributary of the Serepok River), base of Yok Mt. Geographic coordinates 12.8672°N, 107.7075°E, at 194 m a.s.l. in dry, open dipterocarp forest.

**Paratype.**—Female ROM 107765 (field number 42748) collected by B. K. Lim and M. Theberge on 7 June 1997 at the same locality as the holotype. Specimen preserved as a skin, skull (partially damaged during the cleaning process), and partial skeleton. Wing epiphyses unfused and teeth not fully erupted, indicating that this was a juvenile, but volant individual.



**Fig. 4.**—Lateral view of skull of A) *Cassistrellus yokdonensis* sp. nov. (holotype, ROM 107751), B) *C. dimissus* (holotype, BM(NH) 16.4.21.1.), C) *C. dimissus* from Laos (MHNG 1926.053), and D) *C. dimissus* from Nepal (UMMZ 172218). The scale bar at the bottom represents 5 mm.

**Diagnosis.**—*Cassistrellus yokdonensis* sp. nov. is a medium-sized vespertilionid bat (body mass about 15 g) characterized by pointed, narrow wings similar in shape to those of *Nyctalus* species, but not as narrow. The fur is sparse with short hairs, clove brown (Ridgway 1912) dorsally, lighter beige ventrally, and cream colored at the throat. There is no glossy tinge to the fur. The color of the wings and other skin parts is blackish brown. The wing membranes attach to the



distal end of the metatarsus. The calcar extends less than half-way to the tail and has no visible lobe.

Although the dental formula is identical to that of *Eptesicus* species, the skull possesses a pair of deep and well-defined basisphenoid pits and prominent preorbital processes that are otherwise absent from the latter genus. *C. yokdonensis* sp. nov. is morphologically similar to *C. dimissus*, but—in spite of the fact that the known individuals are not fully grown adults—is substantially larger, both externally (e.g., FA 47 mm versus 39–42 mm; [Table 1](#)), and cranially (e.g., maxillary tooththrow length over 6.5 mm versus less than 6.4 mm). *C. yokdonensis* sp. nov. has also a much stronger dentition in general, and subequal small lower premolars, longer more curved upper canines, and procumbent upper incisors compared to its congener. Genetically, *C. yokdonensis* sp. nov. has unique mitochondrial (*Cytb*, *Co1*) and nuclear (*Rag2*) sequences compared to *C. dimissus* from Laos.

*Etymology*.—We propose the name *C. yokdonensis* after the national park where it has been found, in recognition of the importance of protected areas in conserving species and their habitats.

*Description and comparisons*.—Besides its larger mensural dimensions, external and cranial characteristics of *C. yokdonensis* sp. nov. are essentially the same as in the only other known congener (*C. dimissus*), so the diagnostic and distinguishing features are the same as those described for the genus. Compared to *C. dimissus*, *C. yokdonensis* sp. nov. has larger external dimensions ([Table 1](#)), especially longer forearms, hind feet, and ears. Even the immature female (ROM 107765) with unfused wing epiphyses has measurements exceeding those of the largest *C. dimissus*. The general color is clove brown. Wings of *C. yokdonensis* sp. nov. attach to the metatarsus more distally than in *C. dimissus*, and the calcar has no visible lobe.

The skull is rather large (GTL about 18 mm, CM3L about 6.5 mm), but perhaps because the only 2 specimens are not fully adult, the characteristic helmet present in other *Cassistrellus* species is less apparent. But at least when compared to the type of *C. dimissus* (BM(NH) 16.4.21.1), which is also a subadult individual ([Robinson and Kloss 1915](#)), the sagittal crest is less conspicuous in *C. yokdonensis* sp. nov. and hence this could be another distinguishing character ([Fig. 4](#)). Furthermore, as the greatest length of the skull is measured from the bottom of that structure to the tip of incisors, this measurement might be underestimated in these subadult *C. yokdonensis*. The interorbital constriction of the skull is clearly wider in *C. yokdonensis* sp. nov. (IOW 5.0 mm) than in *C. dimissus* (< 4.8 mm).

The dentition of *C. yokdonensis* sp. nov. is very similar to that of *C. dimissus*, with an identical dental formula and a large, unreduced 3rd lower molar. All molars are myotodont. The upper canine of *C. yokdonensis* sp. nov. is long and slender, but the characteristic secondary cusp present on the posterior edge is placed higher, nearly reaching the height of the premolar ([Fig. 4](#)).

*Geographic distribution*.—Currently known only from Yok Don National Park, Dak Lak Province of Vietnam. The 2 specimens were caught shortly after 2100 h as they flew into large

(30 m long by 10 m high) canopy nets deployed in a dry, open dipterocarp forest of lowland regions. Other species of mammals caught in the same nets included *Taphozous*, *Pipistrellus*, *Murina*, *Cynopterus*, *Megaerops*, and *Rhinolophus* bats and several *Hylopetes* flying squirrels. In addition, a paratype specimen of a new species of parachute gecko (*Ptychozoon trinitaterra*) was caught in this net ([Brown 1999](#)).

*Phylogenetic relationships*.—*Cassistrellus yokdonensis* sp. nov. is genetically closely related to *C. dimissus* ([Fig. 1](#)), but differs from it by 9.9% at the *Cytb*, by 10.4% at the *Co1*, and by 0.4% at the *Rag2* genes (K2P distances). Both species appear sister to the genus *Tylonycteris* in all molecular reconstructions, and are part of the Vespertilioninae radiation.

*Nomenclatural statement*.—A life science identifier (LSID) number was obtained for the new genus and species *Cassistrellus yokdonensis*: urn:lsid:zoobank.org:pub:3ED5A281-0FAB-4F4F-842B-C330207BC875.

## DISCUSSION

The combination of new methods to capture bats such as the deployment of harp traps or canopy nets in remote forest areas and the use of molecular characters to complement the morphological diagnosis of specimens is greatly improving our knowledge of bat diversity in tropical areas ([Clare et al. 2007](#); [Francis et al. 2010](#)). Such integrative approaches led to the discovery of many new species, especially in taxonomic groups with relatively conservative morphology such as *Myotis* ([Ruedi et al. 2015](#)) and *Murina* species ([Eger and Lim 2011](#); [Francis and Eger 2012](#); [Ruedi et al. 2012](#); [Soisook et al. 2013](#)). Progress in better understanding systematic relationships of these bats also greatly benefitted from new phylogenetic reconstructions based on extensive DNA character sampling ([Roehrs et al. 2010](#); [Amador et al. 2016](#)).

One necessary step toward communicating these discoveries of genetic diversity is the publication of taxonomic studies conforming to the principles of the International Code of Zoological Nomenclature ([I.C.Z.N. 1999](#)) and based on vouchered specimens, which often lag behind the publication of more general papers. This explains partly the delay between discovery and description of new species ([Fontaine et al. 2012](#)). The discovery of the new genus *Cassistrellus* and the new species *C. yokdonensis* are no exceptions. Long known by a single individual captured in 1913 in peninsular Thailand ([Robinson and Kloss 1915](#); [Thomas 1916](#)), and placed in the genus *Eptesicus*, it was only caught again 77 years later in Nepal ([Myers et al. 2000b](#)), followed 7 years later in Vietnam and again 6 years later in a poorly explored region of northern Laos (present data). Their distant phylogenetic relation to other *Eptesicus* species was revealed by molecular surveys ([Francis et al. 2010](#); [Lack et al. 2010](#)), but it was not until now that the nomenclatural act of raising the *dimissus* lineage to a new genus was taken.

The apparent rarity of *Cassistrellus* specimens in collections (12 known so far) and their widely scattered distribution may be linked to their particular way of living, which makes them elusive to capture. Although no specific studies have been conducted so far on their ecology or feeding behavior,

general information deduced from the capture sites and external morphology of the specimens indicate that they are high-flying, forest species. Indeed, all capture sites are located in lowland forests where bats were either netted high in the canopy (Vietnam) or while the animals were flying low over the rivers shortly after nightfall. At least in Laos, the capture site was far away from any karstic areas or rocky outcrops, suggesting that the animals were roosting in trees rather than in caves. The wing morphology and general characteristics of fur, ears, thumbs, and hind feet of *Cassistrellus* are very similar to those of *Nyctalus* species, which are usually considered as tree dwellers (Rachwald 1992), although few wintering roosts can be found among rocky fissures. The short and pointed wing tips are common features of these species and are typical of fast-flying bats catching insects away from the clutter, e.g., above or along the tree canopy (Norberg and Rayner 1987). These aerial-hawking, forest bats are notably difficult to study via capture, as they escape most traditional catching devices (Kunz and Parsons 2009). This may explain the apparent rarity of *Cassistrellus* in collections. We note that *Eptesicus* bats from the *serotinus* group (Tate 1942; Hill and Harrison 1987) are characterized by longer and broader wings, and hence show lower wing loadings, which enable a more maneuverable flight (Aldridge and Rautenbach 1987; Norberg and Rayner 1987). These bats adopt typically more flexible foraging strategies, being able to hunt both close to the ground and higher in the air near forest canopies (Catto et al. 1995). Serotines also have stronger teeth, enabling them to feed on large, hard-shelled insects such as beetles (Kervyn and Libois 2008). As the *Cassistrellus* dentition is much weaker than in *Eptesicus* of similar body size, *C. dimissus* and *C. yokdonensis* sp. nov. may feed on softer-bodied insects such as moths.

Despite these progresses in understanding systematics and taxonomic status of *C. dimissus* and *C. yokdonensis* sp. nov., karyological characters that are particularly important in classifying Vespertilioninae (Heller and Volleth 1984; Volleth and Tidemann 1989; Volleth et al. 2001; Koubinova et al. 2013) are still unknown. Likewise, no bioacoustic recordings of *Cassistrellus* have been published, but they would be useful to verify our taxonomic conclusions or to record their presence without the need to catch them, as is the case in other, rarely caught fast-flying bats.

As far as is known, the current IUCN Red List of Threatened Species status of “data deficient” assigned to *E. dimissus* [= *C. dimissus*] (Csorba et al. 2016) based on wide distribution from Thailand, Laos, and Nepal may not be appropriate for *C. yokdonensis* sp. nov., which is known only from 1 locality. All the known localities where the Surat and Yok Don helmeted bats have been captured have relatively extensive natural habitats and benefit from varying degrees of legal protection (either as national park or protected area). However, primary lowland forests are being rapidly converted to agricultural lands in the Indomalayan Region, mostly for teak, rubber, or palm oil tree plantations, which certainly reduces their chance of surviving outside protected areas. In particular, the dry open dipterocarp forest in Southeast Asia characteristic of Yok Don National Park warrants more extensive

faunal inventory surveys with the discovery of new species of parachute gecko (Brown 1999) and helmeted bats.

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**APPENDIX 1**  
**Species, tissue or catalog number, location, GenBank accession numbers, and references used in this study.**

Taxon	Tissue collection no.	Museum catalog no.	Locality	GenBank <i>Cytb</i>	GenBank <i>Rag2</i>	GenBank <i>Col</i>	References
<i>Barbastella barbastellus</i>	IZEA3590	MHNG 1804.094	Valais, Switzerland	JQ683210	GU328049		Roehrs et al. (2010)
<i>Barbastella barbastellus</i>			Europe				Rebello et al. (2012)
<i>Barbastella barbastellus</i>	M1187	ZMMU S-174675	Krasnodar, Russia	MG194436	GU328057	JF442793	Kruskop et al. (2012)
<i>Cassidrellus dimissus</i>		MHNG 1926.053	Phongsaly Province, Laos	MG194434	MG194432	MG194430	Lack et al. (2010) and this study
<i>Cassidrellus yokdonensis</i>		ROM 107751	Yok Don National Park, Vietnam	MG194435	MG194433	HM540266	This study
<i>Cassidrellus yokdonensis</i>	TK15160	ROM 107765	Yok Don National Park, Vietnam	EU786865	EU786911		Francis et al. (2010) and this study
<i>Eptesicus furinialis</i>		ROM 103132	Guarico, Venezuela				Juste et al. (2013)
<i>Eptesicus furinialis</i>	TK5893	ROM F38005	Texas, United States	EU786866	EU786912	JF454656	Clare et al. (2011)
<i>Eptesicus fuscus</i>		ROM F38005	Ontario, Canada	AJ841963	EU786885	JF498650	Juste et al. (2013)
<i>Eptesicus hottentotus</i>	M984	MHNG 1972.098	Algeria Forest, South Africa	GQ272582			E. L. Clare, unpublished
<i>Eptesicus nilssonii</i>		Ringed and released	Krasnoyarsk, Russia				Stadelmann et al. (2004b); Juste et al. (2013)
<i>Eptesicus nilssonii</i>			Germany		DQ120811		Artyushin et al. (2009)
<i>Eptesicus pachyomus</i>		ZMMU S-16000a	Russia	EU786849	EU786901	JF442810	Ibáñez et al. (2006)
<i>Eptesicus pachyomus</i>		EBD 25698	Novaphan, Laos				Kruskop et al. (2012)
<i>Eptesicus pachyomus andersoni</i>		ROM 118316	Novaphan, Laos	EU786850	EU786902	HM540268	Juste et al. (2013)
<i>Eptesicus pachyomus andersoni</i>		HNHM 2004.19.28	China	JX902449			Francis et al. (2010); Juste et al. (2013)
<i>Eptesicus pachyomus andersoni</i>		VN11-0076	Vietnam	KX496340			Artyushin et al. (2009)
<i>Eptesicus pachyomus pallens</i>		NMP 90554	Shaanxi, China	EU786841	EU786895		Tu et al. (2017)
<i>Eptesicus serotinus</i>		ZMMU S-191978	Volgograd region, Russia	GQ272579			Juste et al. (2013)
<i>Eptesicus serotinus</i>		ZMMU S-183029	Bryansk region, Russia				Artyushin et al. (2009)
<i>Eptesicus serotinus</i>	M816	MHNG 1807.065	Greece		HM561650	JF442822	Kruskop et al. (2012)
<i>Falsistrellus petersi</i>	EAR6413	FMNH 193513	The Philippines	JX570897	JX570913	MG194431	Roehrs et al. (2010)
<i>Glischropus tylopus</i>	M1568	MHNG 1970.063	Peninsular Malaysia	JX570898	JX570915		Heaney et al. (2012) and this study
<i>Glischropus tylopus</i>	SMF85765		Khammouan, Laos				Heaney et al. (2012)
<i>Hypsugo cadornae</i>	M1183	MHNG 1926.050	Phongsaly Province, Laos	JX570899	GU328061	HM540272	Francis et al. (2010)
<i>Hypsugo cadornae</i>		ROM 110471	Attapu, Laos	AJ504450		HM540636	Lack et al. (2010); Heaney et al. (2012)
<i>Hypsugo savii</i>	IZEA3407	MHNG 1805.007	Valais, Switzerland				Francis et al. (2010)
<i>Hypsugo savii</i>	IZEA3586	MHNG 1804.100	Valais, Switzerland				Stadelmann et al. (2004b)
<i>Hypsugo savii</i>		MIBZPL01295	Central Italy				Roehrs et al. (2010)
<i>Ia ia</i>			Meghalaya, India	DQ302094			Galimberti et al. (2012)
<i>Ia ia</i>			China				Thabab et al. (2007)
<i>Ia ia</i>			Guizhou, China				X. Yuan et al., unpublished
<i>Lasionycteris noctivagans</i>	TK24216	ROM 117763	Texas, United States			HM540662	Francis et al. (2010)
<i>Lasionycteris noctivagans</i>		TTU 56255	New Mexico, United States	L19723	GU328065		Lack et al. (2010)
<i>Lasionycteris noctivagans</i>		LSUMZ 22048	United States				Sudman et al. (1994)
<i>Neoromicia capensis</i>	M963	MVZ 192695	Springbok, South Africa	AJ841965		GU723196	Streicker et al. (2010)
<i>Neoromicia capensis</i>	IVB S1787	MHNG 1972.088	Mt. Assirik, Sénégal	JX276106			Stadelmann et al. (2004b)
<i>Neoromicia capensis</i>	PD63		South Africa				Koubinova et al. (2013)
							Monadjem et al. (2013)

## Appendix 1 (continued)

Taxon	Tissue collection no.	Museum catalog no.	Locality	GenBank <i>Cytb</i>	GenBank <i>Rag2</i>	GenBank <i>Col</i>	References
<i>Neoromicia rendalli</i>	IVB S1212	AM2013.12.4.7	Simenti, Sénégal	JX276206	JX276340		Koubinova et al. (2013)
<i>Neoromicia rendalli</i>	DML13712	MHNG 1956.071	Sierra Leone	JX570901	JX570917	KT598203	Decher et al. (2015)
<i>Nyctalus leisleri</i>	M1473	ZMMU S-167374	Genève, Switzerland	JX570902		JF443043	Heaney et al. (2012)
<i>Nyctalus leisleri</i>	M797	MHNG 1807.050	Russia	JX570902	JX570918		Kruskop et al. (2012)
<i>Nyctalus noctula</i>		ZMMU S-181385	Genève, Switzerland	JX276305		JF443049	Heaney et al. (2012)
<i>Nyctalus noctula</i>	IVB S657		Russia	JX276305	JX276359		Koubinova et al. (2013)
<i>Nycticeinops schlegelii</i>	TK26380	TTU 49536	Dar Salam, Sénégal	KC747697	GU328096		Lack et al. (2010)
<i>Nycticeius humeralis</i>		LSUMZ M8901	Texas, United States				Patrick and Stevens (2014)
<i>Nycticeius humeralis</i>	TK78703	ASNHC 12501	Louisiana, United States				Streicker et al. (2010)
<i>Nycticeius humeralis</i>	NK32223	TTU 79269	United States				Streicker et al. (2010)
<i>Parastrellus hesperus</i>		MSB 75640	Texas, United States	KC747698			Patrick and Stevens (2014)
<i>Parastrellus hesperus</i>	TK90671	MVZ 198302	New Mexico, United States				Streicker et al. (2010)
<i>Parastrellus hesperus</i>	JJ107	TTU 80684	United States	AJ504449	GU328099		Lack et al. (2010)
<i>Perimysotis subflavus</i>	JLS274	FMNH 180236	Texas, United States				Patrick and Stevens (2014)
<i>Philetor brachypterus</i>	JLS517	FMNH 191324	The Philippines	JX570906	JX570922	GU723249	Streicker et al. (2010)
<i>Philetor brachypterus</i>		ROM 102165	The Philippines	JX570907	JX570923	GU723254	Stadelmann et al. (2004a); Lack et al. (2010)
<i>Pipistrellus nathusii</i>	IZEA3406	MHNG 1806.001	Kalimantan, Indonesia	AJ504446			Streicker et al. (2010)
<i>Pipistrellus nathusii</i>	IZEA2830	MHNG 1806.003	Vaud Province, Switzerland				Heaney et al. (2012)
<i>Pipistrellus nathusii</i>		ZMMU S-177904	Vaud Province, Switzerland				Heaney et al. (2012)
<i>Pipistrellus pipistrellus</i>	M1439	MHNG 1807.052	Russia		HM561660		Francis et al. (2010)
<i>Pipistrellus pipistrellus</i>	IVB S1981	MHNG 1806.053	Macedonia, Greece	AJ504443			Stadelmann et al. (2004a)
<i>Pipistrellus pipistrellus</i>	P108	NMP 48437	Geneva, Switzerland				Roehrs et al. (2010)
<i>Pipistrellus pipistrellus</i>		NMP 93719	Valais, Switzerland				Kruskop et al. (2012)
<i>Plecotus macrobullaris</i>			Mbilor, Sénégal	JX276315	JX276350	JF443075	Stadelmann et al. (2004a)
<i>Plecotus macrobullaris</i>			Valais, Switzerland				Roehrs et al. (2010)
<i>Rhynchptesicus nasutus</i>			Spain	NC_027977			Koubinova et al. (2013)
<i>Rhynchptesicus nasutus</i>			Iran	EU786840	GU328106		Lack et al. (2010)
<i>Rhynchptesicus nasutus</i>			Oman	KF019042	KR134391		Alberdi et al. (2015)
<i>Scotoecus hirundo</i>	IVB S1480	MHNG 1926.051	Niériko – bridge, Sénégal	JX276317	EU786894		Juste et al. (2013)
<i>Scotomanes ornatus</i>	M1175	ROM 107594	Phongsaly Province, Laos	JX570910	KF018933		Juste et al. (2013)
<i>Scotomanes ornatus</i>	F42568	ROM 107594	Tuyen Quang, Vietnam				Koubinova et al. (2013)
<i>Scotomanes ornatus</i>	F42568	ROM 107594	Tuyen Quang, Vietnam				Heaney et al. (2012)
<i>Scotophilus heathi</i>	F42769	ROM 107786	Dak Lak, Vietnam	EU750944	HM561656	HM541893	Roehrs et al. (2010)
						HM541926	Francis et al. (2010)
							Trujillo et al. (2009); Francis et al. (2010); Lack et al. (2010)
<i>Scotophilus kuhlii</i>	F44283	FMNH 145684	Sibuyan Island, The Philippines				Lack et al. (2010)
<i>Scotophilus kuhlii</i>	M1538	ROM 110957	Soc. Trang, Vietnam	EU750930	GU328113	HM541932	Lack et al. (2010)
<i>Tylonycteris malayana</i>	M1203	VN11-0022	Phongsaly Province, Laos				Trujillo et al. (2009); Francis et al. (2010)
<i>Tylonycteris malayana</i>		MHNG 1926.059	Vietnam	KX496401	JX570928		Heaney et al. (2012)
<i>Tylonycteris suppressorobustula tonkinensis</i>	IZEA3599	MHNG 1808.017	Phongsaly Province, Laos	KX496441	HM561673	KX496442	Tu et al. (2017)
<i>Vespertilio murinus</i>	M1497	MHNG 1957.087	Valais, Switzerland	AF376834	HM561676		Roehrs et al. (2010); Tu et al. (2017)
<i>Vespertilio murinus</i>		ZMMU S-175195	Russia				Ruedi and Mayer (2001); Roehrs et al. (2010)
<i>Vespertilio murinus</i>			Switzerland	JX570911	JX570929		Heaney et al. (2012)
<i>Vespertilio murinus</i>						JF443150	Kruskop et al. (2012)