A New Species of the Genus Murina (Chiroptera: Vespertilionidae) from the Central Highlands of Vietnam with a Review of the Subfamily Murininae in Vietnam

Article *in* Acta Chiropterologica · December 2015

DOI: 10.3161/15081109ACC2015.17.2.001

Acta Chiropterologica, 17(2): 201–232, 2015
PL ISSN 1508-1109 © Museum and Institute of Zoology PAS
doi: 10.3161/15081109ACC2015.17.2.001

A new species of the genus *Murina* (Chiroptera: Vespertilionidae) from the Central Highlands of Vietnam with a review of the subfamily Murininae in Vietnam

Nguyen Truong Son[1, 8], Gabor Csorba[2], Vuong Tan Tu[1], Vu Dinh Thong[1], Yi Wu[3], Masashi Harada[4], Tatsuo Oshida[5], Hideki Endo[6], and Masaharu Motokawa[7]

[1]*Institute of Ecology and Biological Resources, Vietnam Academy of Sciences and Technology, 18 Hoang Quoc Viet St., Caugiay, Hanoi, Vietnam*
[2]*Department of Zoology, Hungarian Natural History Museum, H1088 Budapest, Baross u.13, Hungary*
[3]*College of Life Science, Guangzhou University, Guangzhou 510006, China*
[4]*Graduate School of Medicine, Osaka City University, Osaka 545-8585, Japan*
[5]*Laboratory of Wildlife Ecology, Obihiro University of Agriculture and Veterinary Medicine, Obihiro 080-8555, Japan*
[6]*The University Museum, The University of Tokyo, 7-3-1 Hongo, Bunkyo-ku, Tokyo 113-0033, Japan*
[7]*The Kyoto University Museum, Kyoto University, Sakyo, Kyoto 606-8501, Japan*
[8]*Corresponding author: E-mail: ntson@iebr.vast.vn*

The subfamily Murininae has high species diversity in Vietnam, but taxonomic studies are limited. In this paper, we describe a new species of the genus *Murina* based on a specimen collected from Ngoc Linh Nature Reserve, Kon Tum Province in the Central Highlands of Vietnam. It is a medium-sized species with '*suilla*-type' dentition. A taxonomic review of Murininae from Vietnam was also conducted based on combined morphological, DNA, and karyological characteristics. Molecular phylogenetic analyses based on the mitochondrial cytochrome *c* oxidase subunit (COI) gene supported the subfamily Murininae, while the genus *Murina* proved to be paraphyletic in relation to the genera *Harpiocephalus* and *Harpiola*. Fourteen species of the genus *Murina*, one species of *Harpiocephalus*, and one species of *Harpiola* are recognized from Vietnam. *Murina tiensa* is regarded as a junior synonym of *M. harrisoni*; strong sexual dimorphism was observed in *M. harrisoni*. Relations between forearm length and total length of skull showed different trends among species and sexes. Karyotypes of *Murina huttoni*, *M. cyclotis*, *M. lorelieae*, *M. beelzebub*, *M. feae*, and *Harpiola isodon* were 2n = 44, FN = 50, while that of *Harpiocephalus harpia* was 2n = 44, FN = 52.

Key words: DNA barcode, karyotype, morphology, taxonomy, tube-nosed bats

Introduction

Species of the subfamily Murininae are small to medium-sized bats of the family Vespertilionidae. They are distributed throughout Asia from north-eastern Pakistan, eastern Siberia, Korea to Japan to northeastern Australia. Diagnostic characters are the combination of: tubular nostrils, thick and woolly fur, furred forearms, hind limbs, proximal parts of wing membranes, and upper surface of interfemoral membrane; and two premolars in both the upper and lower toothrows, where the first premolars are unusually well-developed (Tate, 1941; Corbet and Hill, 1992; Koopman, 1994; Simmons, 2005; Kuo *et al.*, 2006, 2009; Francis and Eger, 2012).

Simmons (2005) listed 17 species of the genus *Murina* Gray, 1842 and subsequent studies described further 21 species, mostly from southern Asia (Csorba and Bates, 2005; Bumrungsri *et al.*, 2006; Csorba *et al.*, 2007, 2011; Kruskop and Eger, 2008; Furey *et al.*, 2009; Kuo *et al.*, 2009; Eger and Lim, 2011; Francis and Eger, 2012; Ruedi *et al.*, 2012; Soisook *et al.*, 2013*a*, 2013*b*; Tu *et al.*, 2015). Inventory studies have been recently conducted in many Southeast Asian countries such as Thailand (10 species — Bumrungsri *et al.*, 2006; Soisook, 2011; Soisook *et al.*, 2013*a*, 2013*b*), Laos (eight species — Francis and Eger, 2012), Cambodia (five species — Csorba and Bates, 2005; Matveev and Csorba, 2007; Csorba *et al.*, 2011; Ith *et al.*, 2011), and Myanmar (four species — Bates *et al.*, 2000), indicating that the genus *Murina* includes interesting forest bats with high species diversity in Asia.

The subfamily Murininae also includes further two genera, *Harpiocephalus* Gray, 1842 and *Harpiola* Thomas, 1915. The validity of the genus

Harpiocephalus has been widely accepted, whereas the taxonomic rank of *Harpiola* has been controversial and considered either a separate genus (Tate, 1941; Bhattacharyya, 2002; Kuo *et al.*, 2006) or a subgenus of *Murina* (Ellerman and Morrison-Scott, 1951; Corbet and Hill, 1992; Koopman, 1994; Simmons, 2005). The phylogenetic reconstruction of Francis *et al.* (2010) based on sequences of the barcoding cytochrome *c* oxidase subunit I (COI) demonstrated that, contrary to the morphological distinctiveness, genetic analyses did not separate *Harpiola* and *Harpiocephalus* from the species of *Murina*.

Vietnam possesses the highest known species diversity of the Murininae in the world. Kuznetsov (2006) and Can *et al.* (2008) listed six species of Murininae in Vietnam, and Kruskop (2013) recognized 12 *Murina*, one *Harpiola*, and one *Harpiocephalus* species from Vietnam after incorporating information from recent studies (Csorba *et al.*, 2007, 2011; Kruskop and Eger, 2008; Furey *et al.*, 2009). Son *et al.* (2015) analysed morphometric variation of the skull of Vietnamese *Murina* and documented considerable interspecific and sexual variation in size and shape of the skull, possibly reflecting food adaptations from interactions of sympatric species. In addition, the existence of sexual dimorphism and the extent of differences among species were documented by Son *et al.* (2015), indicating that the complicated patterns of sexual differences can be the cause of taxonomic confusion among the species.

During the investigation of recently acquired materials, we identified a specimen collected from the Central Highlands of Vietnam that is clearly different from all currently known species of *Murina*. In this study, we describe a new species based on the combined morphological, DNA, and karyological evidences, and review the taxonomic status of all Vietnamese species belonging to the subfamily Murininae. The species diversification of the subfamily and distribution patterns of tube-nosed bats within Vietnam are also discussed.

Materials and Methods

Bats were collected through surveys conducted in 43 protected areas of 28 provinces in Vietnam from 2001 to 2014 (Fig. 1, Table 1, and Appendix I). Three-bank harp traps and mist nets were set at ground level, frequently across trails, streams, and rivers in different habitat types in secondary and primary forests. Mist nets and harp traps were checked every 20 min before dusk from 17:30 until 23:00. Harp traps were left open until around 06:00. Most captured bats were released at the capture site after recording standard measurements. Selected specimens were prepared as voucher specimens. These were fixed in 95% ethanol, followed by preservation in 70% ethanol for about 12 hrs; tissue samples (usually liver or muscle) were preserved in 95% ethanol.

A total of 252 specimens were examined in this study (Appendix II). Voucher specimens are kept in the Institute of Ecology and Biological Resources, Hanoi, Vietnam (IEBR); Hungarian Natural History Museum, Budapest, Hungary (HNHM); Harrison Institution, Sevenoaks, United Kingdom (HZM); Royal Ontario Museum, Toronto, Canada (ROM); Natural History Museum, London, United Kingdom (BMNH); Zoological Museum at Moscow University, Moscow, Russia (ZMMU); and Muséum National d'Histoire Naturelle, Paris, France (MNHN). Chinese specimens deposited in the College of Life Science, Guangzhou University, Guangzhou, China (IBHG) were also investigated.

Morphological Examination

Terminology of external, skull, and dental morphology followed Bates and Harrison (1997), Csorba and Bates (2005), Csorba *et al.* (2007, 2011), and Furey *et al.* (2009). Abbreviations used for the dental nomenclature were incisor (I/i_n), canine (C/c), premolar (P/p_n), and molar (M/m_n), with premaxillary and maxillary teeth denoted by uppercase and mandibular teeth by lowercase letters. Only adult specimens (age was determined following Anthony, 1988) were used for statistical analyses.

The following external measurements were taken to the nearest 0.1 mm: HB, head and body from the tip of nose to the

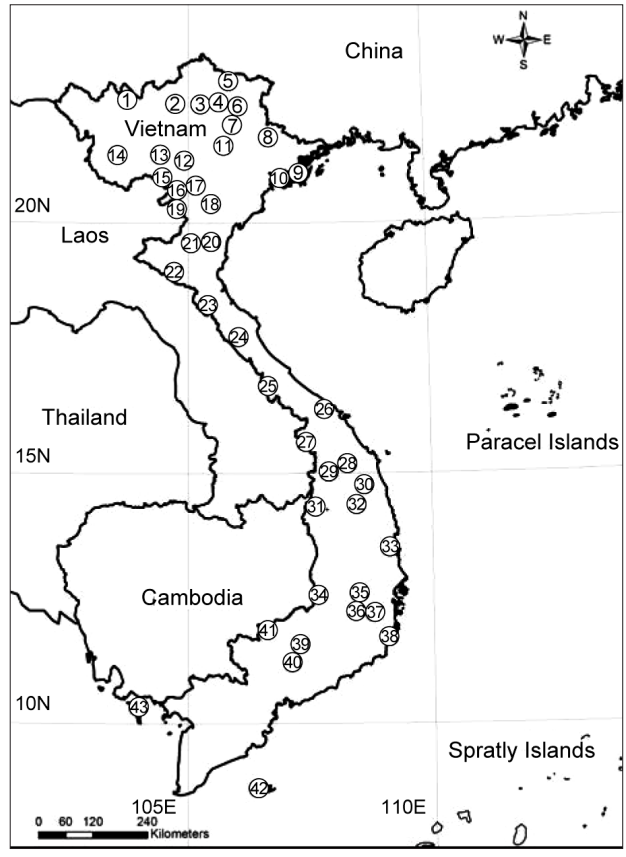

Fig. 1. Map of localities for specimens of the subfamily Murininae from Vietnam. Locality names are given in Appendix I

TABLE 1. Distribution of the subfamily Murininae from Vietnam. Locality numbers correspond to those in Fig. 1 and Appendix I. Species are arranged following the overall skull size (in decreasing order; species names abbreviated to the first 3-4 letters). Number of provinces where the species occurs is shown in parentheses

Locality number	Province	Number of species	Species (Number of provinces)														
			H.har (10)	M.harr (8)	M.leu (1)	M.fio (7)	M.hut (9)	M.cyc (23)	H.iso (2)	M.lor (1)	M.ann (10)	M.bee (4)	M.wal (4)	M.fea (18)	M.kon (1)	M.ele (10)	M.harp (1)	M.chr (2)
1	Lao Cai	5	x				x		x		x							x
2	Ha Giang	3						x						x		x		
3	Tuyen Quang	4	x					x			x			x				
4, 6	Bac Kan	5	x	x				x						x		x		
5	Cao Bang	5	x				x	x								x		x
7	Thai Nguyen	1												x				
8	Lang Son	1	x															
9	Quang Ninh	1						x										
10	Hai Phong	2		x				x										
11	Vinh Phuc	4	x	x				x						x				
12	Phu Tho	4		x				x						x		x		
13, 14, 15	Son La	5		x				x			x			x		x		
16, 17, 19, 20	Thanh Hoa	5		x				x			x			x		x		
18	Ninh Binh	2						x						x				
21, 22	Nghe An	7	x	x	x		x	x			x			x				
23	Ha Tinh	1												x				
24	Quang Binh	5	x			x		x						x		x		
25	Quang Tri	6				x	x	x			x	x		x				
26	Thua Thien-Hue	2						x						x				
27, 28	Quang Nam	5				x	x				x			x		x		
29, 31	Kon Tum	11	x			x	x	x	x	x	x	x		x	x	x		
30	Quang Ngai	5				x		x			x	x				x		
32	Gia Lai	4				x		x				x		x				
33	Binh Dinh	1						x										
34, 35	Dak Lak	3		x			x						x					
36	Lam Dong	4	x				x	x									x	
37	Khanh Hoa	1					x											
38	Ninh Thuan	1											x					
39, 40	Dong Nai	4				x		x					x	x				
41	Binh Phuoc	2						x			x							
42	Ba Ria-Vung Tau	1						x										
43	Kien Giang	1											x					

base fundament; FA, forearm length from the extremity of the elbow to the extremity of the carpus with the wings folded; T, tail length from the tip of tail to its base fundament; HF, hind foot from the tip of the longest digit, excluding claw, to the extremity of the heel, behind the os calcis; TIB, tibia length from the knee joint to ankle; E, ear length from the lower border of external auditory meatus where it joins with the body to the tip of pinna; TRAGUS, tragus length from the lower posterior emargination to the tip of the tragus; and body mass (in gram).

Craniodental and mandibular measurements were taken to the nearest 0.01 mm following Son *et al.* (2015): STOTL, total length of skull from the anterior rim of the alveolus of the first upper incisor to the most projecting point of the occipital region; CCL (condyle-canine length), from the exoccipital condyle to the most anterior part of the canine; C1C1W, greatest width across the outer borders of the upper canines; M3M3W, greatest width across the outer crowns of the last upper molars; ZYW (zygomatic width), greatest width of the skull across the zygomatic arches; MAW (mastoid width), greatest distance across the mastoid region; IOW (interorbital width), least width of the interorbital constriction; 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); CM3L (maxillary toothrow length), from the front of upper canine to the back of the crown of the third molar; CP4L (upper canine-premolar length), from the front of the upper canine to the back of the crown of the posterior premolar; ML (mandible length), from the anterior rim of the alveolus of the first lower incisor to the most posterior part of the condyle; cm3L (mandibular toothrow length), from the front of the lower canine to the back of the crown of the third lower molar; cp4L (lower canine-premolar length), from the front of the lower canine to the back of the crown of the posterior premolar; 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.

Multivariate Analyses

To study individual variation in *M. harrisoni*, we used all 15 craniodental and mandibular measurements to conduct two PCA analyses with the software PAST (Hammer *et al.*, 2001) using (1) raw data to assess size factors using the PC1 score that represents overall size (Barlow *et al.*, 1995; Lindenfors *et al.*, 2007), and (2) standardized data (raw score/geometric mean) to assess the shape factor (Jungers *et al.*, 1995) using each of the PC scores that have eliminated size factors. Both the raw data and standardized data were log-transformed (Blackith and Reyment, 1971; Reyment, 1971).

DNA Barcoding

Total genomic DNA was extracted from muscle samples using the DNeasy Blood and Tissue Kit (Qiagen, California) following the manufacturer's protocol. A 657 bp fragment of the mitochondrial COI gene was amplified and sequenced with the primers LCO1490 and HCO2198 (Hebert *et al*., 2003). The polymerase chain reactions (PCR) were carried out in a volume of 10 mml of HotStarTaq mastermix (Qiagen, California), 5 ml of water, 2 ml of each primer at 10 pmol/µl and 2 ml of DNA. PCR condition was: 95°C for five minutes to active Hot Star Taq; with 40 cycles at 95°C for 30s, 45° for 45s, 72°C for 60s; and the final extension at 72°C for six minutes. PCR products were purified using GeneJET^{TM} PCR Purification kit (Fermentas, Canada) and then were sent to Macrogen Inc. (Seoul, South Korea) for sequencing. Sequences were edited and assembled using Codoncode Alignment ver. 5.0.2 (CodonCode Corporation).

The new COI sequence (GenBank accession number KT820760) was compared to those of 25 identified species of the subfamily Murininae in the EMBL, GenBank, DDBJ, and BOLD nucleotide databases (Appendix III). Phylogeny of the subfamily Murininae was reconstructed using the Bayesian method. Based on previous studies (Hebert *et al*., 2003), *Myotis muricola* and *Kerivoula hardwicki* were used as outgroups. DNA sequences were aligned manually on PhyDE v0.9971 (Müller *et al.*, 2010). The COI dataset represents a total alignment of 657 nucleotides and 120 taxa. The best-fitting model of sequence evolution was selected under jModelTest using the Akaike information criterion. Bayesian analyses were then conducted using the selected GTR+I+G model on MrBayes v3.2 (Hebert *et al*., 2003). Posterior probabilities (*PP*) were calculated using four independent Markov chains run for 10,000,000 Metropolis-coupled MCMC generations, with tree sampling every 1,000 generations, and a burn-in of 25%. Mean pairwise distances were calculated with PAUP version 4b10 (Swofford, 2003) using Kimura's two-parameter (K2P) model.

Karyotype Analyses

Chromosomal preparations were made with culture cells of tail bone or ear tissue following the method of Harada and Yosida (1978). The tissue sample was cultured with Eagle's MEM medium supplemented with 12% calf serum, 3% calf serum and a few non-essential amino acids (l-glutamine, l-serine, sodium pyruvate). Diploid chromosome number (2n) and fundamental number (FN, as the total number of autosomal arms) was then calculated.

Results

The Bayesian tree reconstructed from the nucleotide alignment of COI sequences (Fig. 2) supported the monophyly of the subfamily Murininae (*PP* = 1) that included the genera *Murina*, *Harpiocephalus*, and *Harpiola*; however, the genus *Murina* was proved to be paraphyletic in relation to the genera *Harpiocephalus* and *Harpiola*. The species relationships within Murininae were poorly supported (*PP* < 0.7), similar to findings of Francis *et al.* (2010) and Tu *et al.* (2015). Only the following sister relationships were supported with posterior probabilities > 90%: *Harpiocephalus harpia* and *Murina* sp. nov. (IEBR-M5697; to be described in this paper); *M. suilla* and *M. walstoni*; *M.* cf. *cyclotis* from India and *M. guilleni*; *M.* cf. *cyclotis* from India / *M. guilleni* / *M. fionae* / *M. cyclotis* / *M. peninsularis*; *M. gracilis* and *M. recondita*; *M. eleryi* / *M. gracilis* / *M. recondita* / *M. balaensis*; *M. harrisoni* / *M. huttoni* / *M. ussuriensis*; *M. chrysochaetes* and

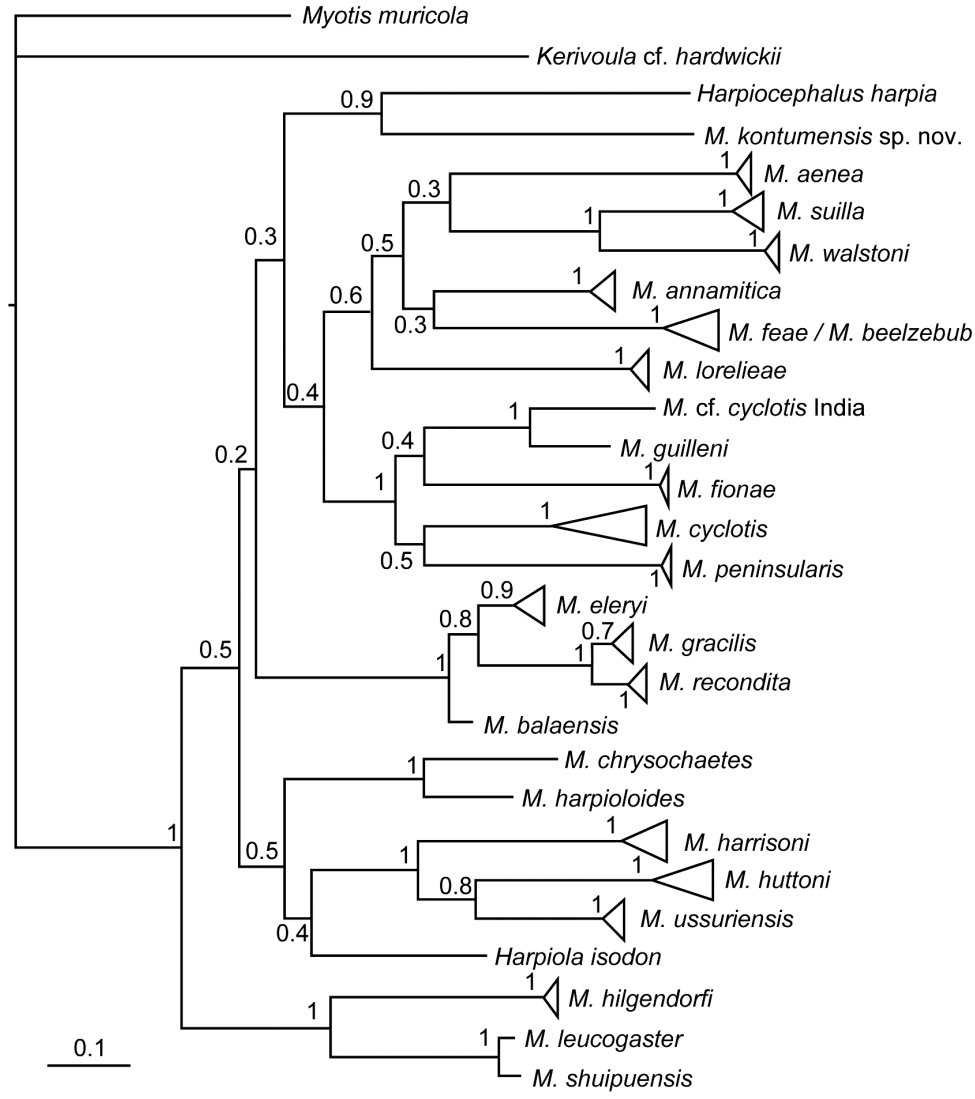

FIG. 2. Bayesian tree of the subfamily Murininae reconstructed based on 120 sequences of the mitochondrial cytochrome *c* oxidase subunit I (COI) gene, with posterior probabilities (*PP*) values. *Murina feae* and *M. beelzebub* are based on data from Francis *et al.* (2012), collectively reported as *M. feae*

M. harpioloides; *M. leucogaster* and *M. shuipuensis*; *M. hilgendorfi* / *M. leucogaster* / *M. shuipuensis*. Although the monophyly of the genus *Murina* was not supported, the morphological distinctness of the three genera (*Harpiocephalus, Harpiola*, and *Murina*) was clear, and was therefore recognized as valid.

TAXONOMIC ACCOUNTS

Genus *Murina* Gray, 1842

Diagnostic characters

Small to medium-sized bats with tubular nostrils and dense woolly pelage. I2/3 C1/1 P2/2 M3/3 = 34. Height of upper incisors is distinctly less than that of the corresponding canines. I3 is not contact with C. M3 is developed.

Taxonomic notes

Two morphogroups, namely '*suilla*-group' and '*cyclotis*-group', differing in the relative size and position of the upper incisors, canines, premolars, and ratio of upper canine and second upper premolar have been widely accepted (Corbet and Hill, 1992; Koopman, 1994; Csorba and Bates, 2005; Csorba *et al.*, 2007; Furey *et al.*, 2009; Kuo *et al.*, 2009; Soisook *et al.*, 2013*b*; Son *et al.*, 2015). As an important characteristic, crown area of the upper canine is less than that of P4 in the '*suilla*-group',

and is equal to or exceeds that of P4 in the '*cyclotis*-group'. Although we recognize the usefulness of these characteristics for identification of the species, these morphogroups do not represent separate phylogenetic lineages. Therefore, morphological characteristics are referred hereafter as '*suilla*-type' dentition and '*cyclotis*-type' dentition without using the term 'group'.

Murina kontumensis Son, Csorba, Tu and Motokawa, sp. nov. (Fig. 3)

Holotype

IEBR-M5697, field number B20140920.14. Adult female, skin and skull, collected from Ngoc Linh Nature Reserve, Xop commune, Dak Glei district, Kon Tum province, Vietnam (15°05'30N, 107°51'35E; Fig. 1, No. 22), 1,780 m a.s.l.; collected by Vuong Tuan Tu, Masaharu Motokawa and Nguyen Truong Son on 20 September 2014. Measurements (in mm) are as follows, HB: 40.00, FA: 32.28, T: 38.50, HF: 7.60, TIB: 16.20, E: 18.70, TRAGUS: 8.74, STOTL: 14.98, CCL: 13.29, C1C1W: 3.66, M3M3W: 5.30, ZYW: 8.53, MAW: 7.55, IOW: 3.94, BCW: 7.32, BCH: 6.65, CM3L: 5.01, CP4L: 2.28, ML: 10.10, cm3L: 5.56, cp4L: 2.18, CPH: 3.47, and body mass: 5 g (Table 3).

Diagnosis

Medium-sized, with '*suilla*-type' dentition. Head is with a distinct facemask, dark brown around the eyes, with a contrasting whitish collar around the neck. General impression of dorsal pelage is brownish grey with scattered golden hairs; ventral fur is light brown. Plagiopatagium is attached to the base of the first claw of the outer toe. Skull is domed, and sagittal and lambdoid crests are evident. I2 clearly is anterior to I3. Crown area of P2 is one-half of P4; crown area of upper canine is less than that of P4; P2 is antero-posteriorly compressed. The mesostyles of M1 and M2 are well developed.

Description of the holotype

Medium-sized, with '*suilla*-type' dentition (Figs. 3 and 4, Tables 2 and 3). FA 32.28, STOTL 14.98, and body mass 5.0 g. On the dorsum, the basal portions of the hairs are dark brown and followed by a light brown section before terminating in a distinctly darker brownish-grey tip. Guard hairs with shiny golden tips are scattered on the head and behind the ears, and more sparsely over the back. Ventrally, hairs are grey for the proximal one-third, whereas the remaining upper portion is light brown.

Head is with a distinct facemask, dark brown around the eyes, with a contrasting whitish collar around the neck. Ear is 18.70 mm long and 11.25 mm wide, having a slight emargination along its posterior border; the tragus is 8.74 mm in length, the widest point near the base is 2.10 mm. The upper surface of hind limbs, feet and uropatagium are densely covered in short, uniformly shiny golden brown hairs. The ventral surface of the uropatagium is covered in uniformly golden white hairs, some of which are also present on the plagiopatagium adjacent to the body. Plagiopatagium attached to base of the claw of the first toe.

Skull and dentition (Figs. 3, 5, 6, and Table 3). Skull is medium-sized. The rostrum is slightly shortened and domed, and from the top of skull to nasal bone, is relatively steep. Braincase is domed. Zygoma is not strong. Length of second upper premolar is half the length of the canine. The upper toothrow is convergent anteriorly (C1C1W/M3M3W, 0.70). One half of I2 is obscured in the lateral view. I3 is not in contact with upper C. The basal area of upper C is less than that of P4, whereas its height is greater. In the occlusal view, upper C is relatively circular. P2 is strongly compressed, wider than long, with a small cusp on the anterior inner cingulum. Its basal area and height are approximately half or slightly less than that of P4. Mesostyles of M1 and M2 are well developed comparable in height to metastyle and parastyle, giving a distinct W-shape to the surface.

Lower c exceeds p4 in height and is equal or greater in basal area; p2 has less than half the basal area of p4 and attains more than two-thirds of its height. Talonids of m1 and m2 are wider than their trigonids. Hypoconid of m2 distinctly exceeds its entoconid in height, whereas entoconid of m2 is lower than hypoconid and metaconid.

Etymology

The specific epithet *kontumensis* refers to Kon Tum Province, from where the holotype was collected.

COI sequences

The Bayesian tree reconstructed from the nucleotide alignment of COI sequences determined that *M. kontumensis* sp. nov. was distantly related to 25 examined species of the subfamily Murininae, forming sister relationship with *H. harpia* (Fig. 2). The mean pairwise distances between *M. kontumensis* sp. nov. and other species of Murininae varied between 16.2% to 20.5%, supportive as representing a distinct species.

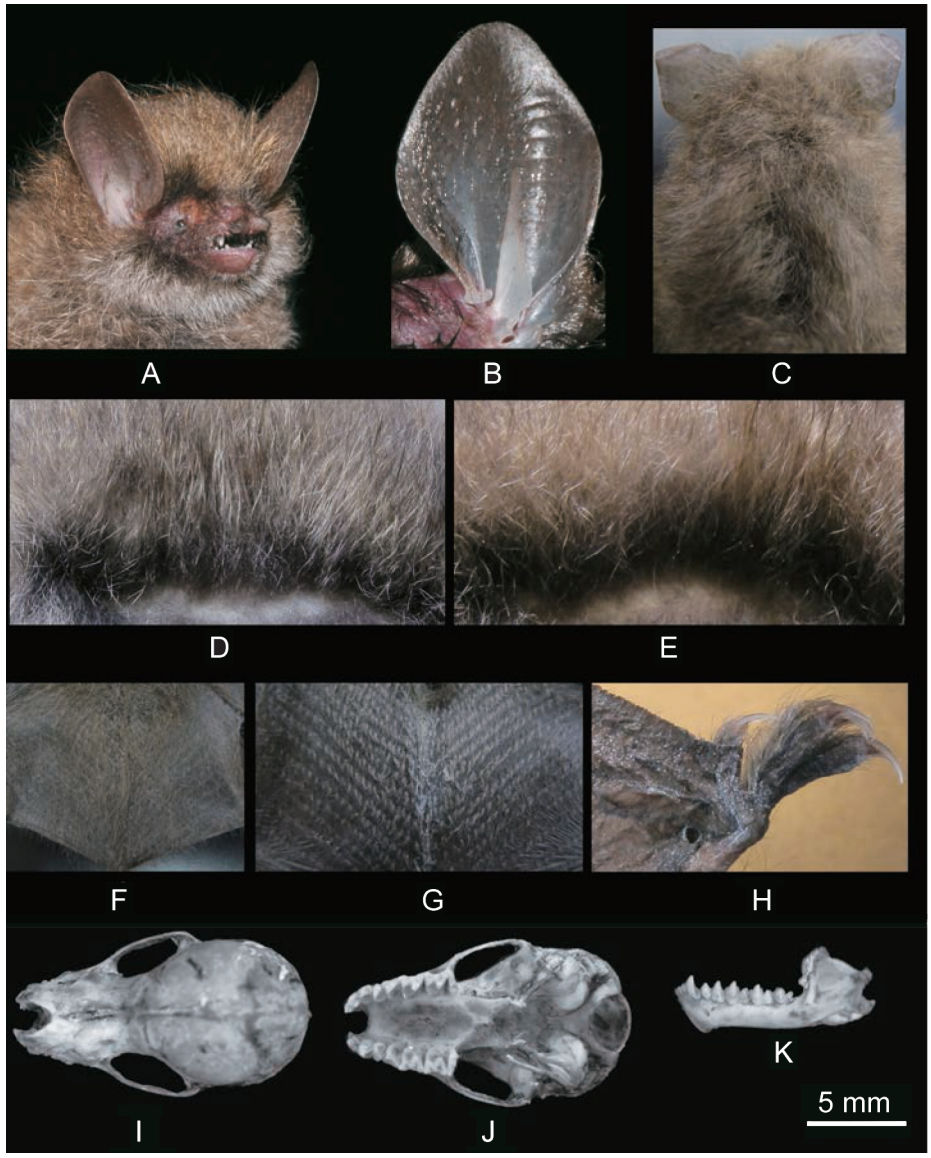

FIG. 3. *Murina kontumensis* sp. nov. (holotype, IEBR-M5697): A — face; B — ear and tragus; C — dorsal pelage; D — ventral fur; E — dorsal fur; F — upper surface of uropatagium; G — ventral surface of uropatagium; H — plagiopatagium and the first claw; I — dorsal view of skull; J — ventral view of skull; K — lateral view of mandible

Comparative material

Murina annamitica: IEBR-M3167, M2181, M4131, M2997, M3650, HNHM TJO 423, HNHM BHH 12; *M: beelzebub*: IEBR-M5760/HNHM. 2007.50.6; *M. chrysochaetes*: ZMMU S186699; *M. cyclotis*: IEBR-M3128, M3316, M3646; *M. feae*: IEBR-M4214, M3154, HNHM QT 003, HNHM PHV 23; *M. eleryi*: HNHM. 2007. 51.1, HNHM. 2007.28.2, IEBR-M4070; *M. gracilis*: HNHM 2005. 1.1; *M. harpioloides*: ZMMU-S-173401, IEBR-M5718; *M. lorelieae*: ROM 116171; MNHN 2013-1078, VN11-1120, VN11-1223, VN11-1161, IEBR-M5648, M5651, M5656, M5662; HNHM. B2014 0915.5, 20140915.7; *M. recondita:* HNHM 2005. 36.1; *M. suilla*: HNHM 2000.13.2; *M. walstoni*: HNHM 2010.20.1, IEBR-M4592, M2920, M2479.

Comparison with other taxa

Murina kontumensis sp. nov. differs from all known Southeast Asian species having '*suilla*-type' dentition by the combination of the brownish dorsal pelage, scattered shiny golden guard hairs on the head, the dorsum and the dark brown colouration around the eyes, a contrasting whitish collar around the neck, more domed skull, and narrow nasal sinus (Figs. 4–6).

Compared to other dorsally brownish-reddish species with golden-tipped guard hairs,

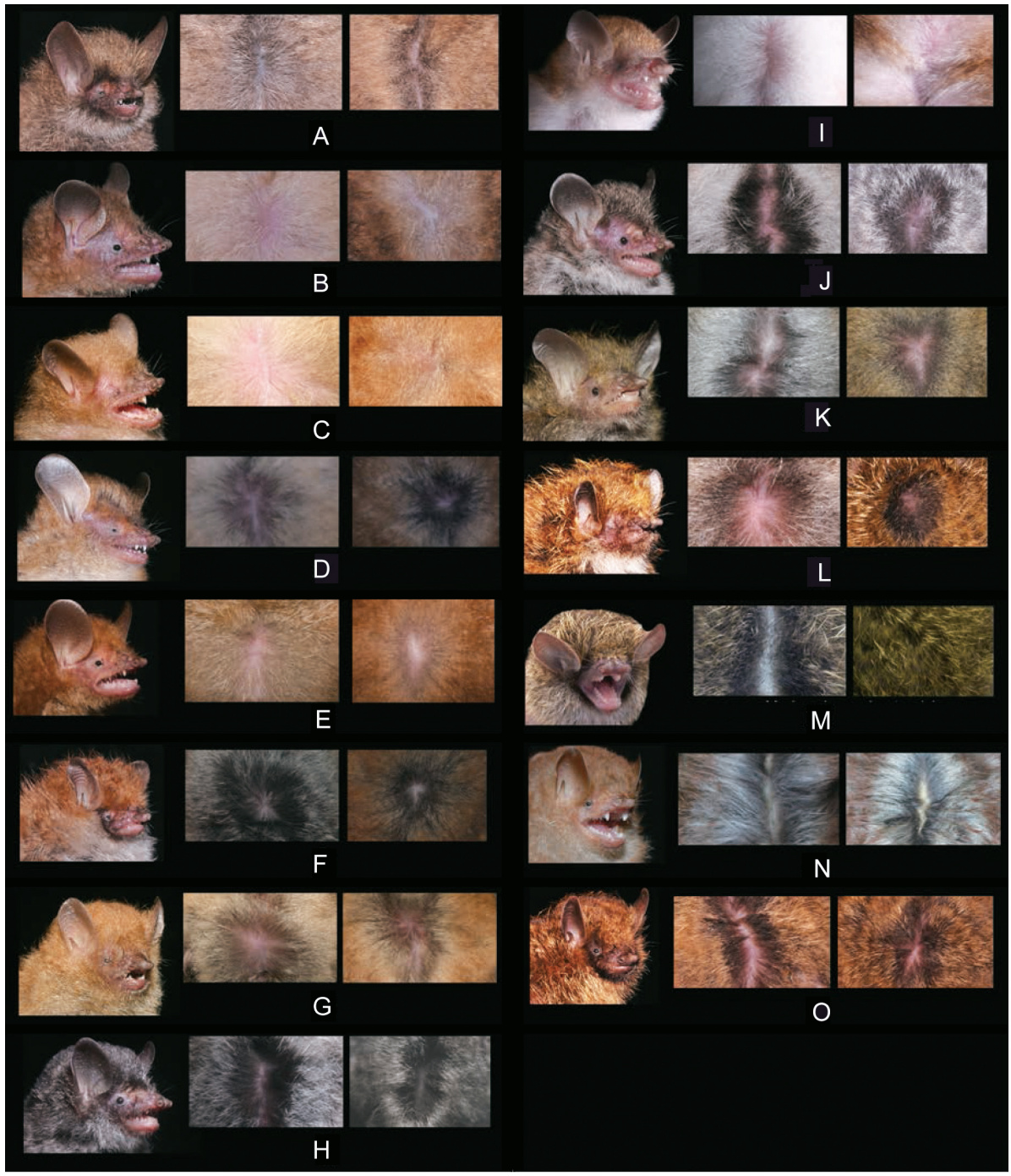

Fig. 4. Face (left), ventral fur (middle), and dorsal fur (right) of specimens from species in the subfamily Murininae from Vietnam: A — *M. kontumensis* sp. nov. (holotype, IEBR-M5697); B — *M. harrisoni* (IEBR-M3299); C — *M. fionae* (IEBR-M3080); D — *M. huttoni* (IEBR-M5693); E — *M. cyclotis* (IEBR-M4223); F — *M. lorelieae* (IEBR-M5656); G — *M. annamitica* (IEBR-M3034); H — *M. beelzebub (*IEBR-M3904); I — *M. walstoni* (IEBR-M4592); J — *M. feae* (IEBR-M3264)); K — *M. eleryi* (IEBR-M4070); L — *M. harpioloides* (IEBR-M5806); M — *M. chrysochaetes* (ROM MAM 116181); N — *H. harpia* (IEBR-M6037 left, IEBR-M5661 middle and right); O — *H. isodon* (IEBR-M5436)

M. kontumensis sp. nov. further differs from *M. eleryi* by its brown-tipped ventral fur (white tipped in *M. eleryi*), and from *M. gracilis* by its well-furred uropatagium (almost naked in *M. gracilis*).

Compared with the dorsally reddish and brownish species with no shiny guard hairs, *M. kontumensis* sp. nov. is smaller than *M. lorelieae* (Tables 2 and 4), *M. recondita* (FA mean 30.9, GLS mean 15.48 —

TABLE 2. Mean, range, and sample size (in italics) for external measurements (mm) and body mass (g) of bats of the subfamily Murininae from Vietnam. The measurements for *M. leucogaster* follow Hendrichsen *et al.* (2001)

Species	Sex	FA		HB		T		HF		E		TIB		Body mass	
		$\bar{x}$	Range	$\bar{x}$	Range	$\bar{x}$	Range	$\bar{x}$	Range	$\bar{x}$	Range	$\bar{x}$	Range	$\bar{x}$	Range
M. kontumensis sp. nov.	♀	32.3	–	40.0	–	38.5	–	7.6	–	18.7	–	16.2	–	5.0	–
M. leucogaster	♀	41.8	–	–	–	40.0	–	9.8	–	14.2	–	18.8	–	8.8	–
M. harrisoni	♂	35.30	34.0–36.7 *11*	44.27	38.9–50.0 *3*	39.50	35.8–45.5 *3*	8.20	7.4–9.0 *3*	14.60	13.5–15.5 *3*	19.33	19.0–19.5 *3*	8.4	–
	♀	38.18	35.6–40.1 *10*	40.3	44.9	40.1	41.7	8.1	10.2	15.4	18.8	18.6	21.0	10.5	–
M. fionae	♂	35.32	34.2–36.4 *6*	45.62	42.1–48.2 *6*	39.95	37.0–44.5 *6*	8.17	6.8–9.3 *6*	14.32	13.7–14.6 *6*	19.20	18.5–20.8 *6*	7.87	7.5–9.0 *6*
	♀	37.9	–	51.3	–	41.7	–	9.1	–	16.0	–	20.7	–	12.0	–
M. huttoni	♂	33.36	32.0–36.0 *8*	46.21	44.0–50.0 *7*	37.57	31.0–41.5 *7*	7.30	6.6–8.6 *7*	16.32	14.0–17.0 *8*	16.71	16.7–16.7 *8*	5.89	5.3–6.3 *5*
	♀	34.34	33.1–35.5 *10*	46.26	40.0–53.0 *10*	36.02	32.0–42.5 *10*	7.89	7.0–8.9 *10*	16.30	15.9–17.0 *10*	16.74	16.0–17.7 *10*	6.36	5.3–8.0 *10*
M. cyclotis	♂	30.33	28.9–32.0 *33*	40.98	38.0–48.0 *33*	35.13	31.8–38.7 *33*	7.27	6.3–8.5 *33*	14.55	12.3–17.0 *33*	17.01	15.9–17.8 *36*	5.01	4.1–6.0 *19*
	♀	34.37	32.1–36.3 *26*	44.07	40.0–51.0 *26*	38.33	32.1–43.5 *26*	7.53	6.3–8.60 *26*	15.01	12.5–18.6 *26*	18.27	15.0–20.1 *26*	6.82	4.7–8.2 *16*
M. lorelieae	♂	33.72	33.0–34.5 *7*	39.14	37.0–41.0 *7*	35.00	31.0–38.0 *7*	6.71	6.0–7.5 *7*	15.10	14.0–16.0 *7*	33.72	33.0–34.5 *7*	4.87	4.2–6.6 *x*
	♀	35.25	34-9–35.6 *3*	44.40	43.3–45.5 *3*	39.70	38.4–41.0 *3*	8.45	8.4–8.5 *3*	15.80	15.6–16.0 *3*	19.20	19.1–19.3 *3*	6.00	5.5–6. *3*
M. annamitica	♂	30.91	29.4–32.1 *11*	40.32	36.2–48.0 *10*	35.72	32.5–38.8 *10*	6.74	5.9–8.1 *10*	12.86	11.9–14.2 *10*	16.58	15.4–17.4 *11*	5.66	4.3–7. *8*
	♀	32.12	27.0–34.6 *10*	43.70	38.2–55.0 *10*	36.80	32.4–40.3 *10*	7.15	6.2–8.1 *10*	13.09	11.9–15.0 *10*	17.19	16.0–18.0 *10*	6.75	5.3–8.0 *10*
M. beelzebub	♂	34.43	34.4–34.5 *3*	42.67	40.0–44.0 *3*	38.90	36.8–41.4 *3*	7.13	6.6–8.0 *3*	14.13	14.1–14.2 *3*	18.57	18.1–19.4 *3*	3.0	5.5
	♀	36.45	36.0–37.3 *5*	44.37	41.6–49.0 *5*	39.60	33.0–44.8 *5*	6.80	5.5–8.0 *5*	13.73	13.2–14.0 *5*	18.84	18.0–19.6 *5*	3.0	5.5
M. walstoni	♂	33.16	32.7–34.1 *3*	35.41	34.8–35.9 *3*	30.93	29.8–32.5 *3*	6.52	6.1–7.0 *3*	13.01	12.5–14.0 *3*	14.08	13.4–15.0 *3*	4.40	4.2–4.6 *3*
	♀	33.40	32.6–33.5 *3*	40.22	35.2–43.5 *3*	28.79	26.6–30.0 *3*	6.36	6.1–6.5 *3*	12.90	12.1–14.1 *3*	14.66	13.9–15.6 *3*	4.6	–
M. feae	♂	30.12	27.5–33.4 *17*	38.29	33.7–43.0 *13*	34.89	31.4–39.5 *13*	6.86	6.0–8.4 *14*	12.99	11.5–14.3 *14*	16.57	15.7–18.1 *17*	4.22	3.5–5.3) *8*
	♀	31.40	28.1–34.3 *16*	38.69	32.8–43.5 *16*	35.46	30.0–41.6 *16*	6.83	6.1–8.0 *16*	12.90	11.0–15.0 *16*	16.95	15.6–17.8 *16*	4.20	3.9–4.4 *6*
M. eleryi	♂	28.23	27.3–29.4 *7*	33.19	31.5–36.2 *3*	29.52	26.5–32.3 *7*	6.40	5.2–7.7 *7*	12.20	11.5–13.3 *7*	14.05	13.0–15.1 *7*	4.03	2.5–5.0 *6*
	♀	29.87	28.6–31.3 *8*	35.8	39.0	29.87	27.3–32.1 *8*	6.75	6.0–7.4 *8*	12.57	11.7–13.3 *8*	13.96	13.2–15.0 *8*	4.79	4.0–5.5 *7*
M. harpioloides	♀	29.7	29.8	34.5	35.0	27.0	30.5	6.5	–	12.3	–	13.0	14.4	4.2	–
M. chrysochaetes	♀	28.6	29.8	40.0	41.0	24.0	26.0	5.5	5.6	12.0	12.6	12.6	12.7	4.0	4.4
H. harpia	♂	49.4	49.5	55.0	57.0	40.0	50.0	11.0	11.2	17.0	18.0	22.0	24.0	16.0	24.0
	♀	52.8	50.9–54.9 *3*	59.7	59.0–61.0 *3*	48.6	47.7–50.0 *3*	11.5	11.0–12.0 *3*	17.7	17.0–18.0 *3*	22.7	22.0–23.5 *3*	27.1	25.0–30.2 *3*
H. isodon	♂	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	♀	37.3	–	44.0	–	36.0	–	7.5	–	15.0	–	15.0	–	7.0	–

TABLE 3. Craniodental measurements ($\bar{x} \pm$ SE, range; in mm) of *M. kontumensis* sp. nov., *M. lorelieae*, *M. harrisoni*, *H. harpia*, and *H. isodon* (specimens of *M. harrisoni* from Vietnam, Cambodia, China, and Thailand, and those for other species from Vietnam)

Parameter	*M. kontumensis* sp. nov.	*M. lorelieae*		*M. harrisoni*		*H. harpia*		*H. isodon*
	♀ ($n = 1$)	♂♂ ($n = 7$)	♀♀ ($n = 3$)	♂♂ ($n = 10$)	♀♀ ($n = 11$)	♂♂ ($n = 3$)	♀♀ ($n = 2$)	♀ ($n = 1$)
STOTL	14.98	16.12 ± 0.19 (15.83–16.39)	16.54 ± 0.29 (16.33–16.74)	17.85 ± 0.46 (16.95–118.39)	18.64 ± 0.63 (17.46–19.43)	22.26 ± 0.07 (21.45–23.07)	22.82, 23.25	17.09
CCL	13.29	13.96 ± 0.20 (13.55–14.14)	13.96 ± 0.20 (13.55–14.14)	15.92 ± 0.25 (15.46–16.25)	16.62 ± 0.49 (15.96–17.16)	19.42 ± 0.73 (18.90–19.42)	20.01, 20.26	14.95
C1C1W	3.66	3.86 ± 0.06 (3.74–3.92)	3.86 ± 0.06 (3.74–3.92)	4.64 ± 0.21 (4.16–4.94)	5.00 ± 0.19 (4.66–5.31)	6.74 ± 0.41 (6.45–7.03)	6.74, 7.17	4.26
M3M3W	5.30	5.43 ± 0.09 (5.29–5.58)	5.43 ± 0.09 (5.28–5.58)	5.81 ± 0.18 (5.63–5.98)	6.12 ± 0.21 (5.78–6.44)	6.57 ± 0.46 (6.24–6.89)	7.23, 7.75	5.65
ZYW	8.53	8.97 ± 0.14 (8.78–9.17)	9.25 ± 0.28 (9.05–9.45)	10.32 ± 0.25 (9.97–10.62)	9.29 ± 0.38 (10.13–11.47)	13.73 ± 1.15 (12.92–14.54)	14.48, 15.09	9.61
MAW	7.55	7.68 ± 0.10 (7.76–7.89)	7.92 ± 0.22 (7.76–8.07)	8.85 ± 0.29 (8.31–9.31)	9.29 ± 0.38 (8.34–9.61)	11.23 ± 0.74 (10.70–11.75)	11.45, 11.98	8.12
IOW	3.94	4.21 ± 0.04 (4.17–4.29)	4.29 ± 0.15 (4.17–4.39)	4.36 ± 0.12 (4.23–4.58)	4.48 ± 0.09 (4.30–4.58)	5.57 ± 0.21 (5.42–5.72)	5.57, 6.05	5.12
BCW	7.32	7.46 ± 0.11 (7.33–7.62)	7.68 ± 0.32 (7.45–7.90)	7.81 ± 0.22 (7.46–8.11)	7.94 ± 0.29 (7.76–8.22)	9.42 ± 0.34 (9.18–9.66)	9.60, 10.23	7.72
BCH	6.65	6.65 ± 0.26 (6.20–6.94)	6.53 ± 0.08 (6.45–6.54)	6.49 ± 0.18 (6.16–6.78)	6.74 ± 0.29 (6.22–7.23)	9.51 ± 0.36 (9.25–9.76)	9.74, 10.12	7.77
CM3L	5.01	5.30 ± 0.06 (5.21–5.40)	5.55 ± 0.13 (5.46–5.64)	6.11 ± 0.17 (5.82–6.31)	6.53 ± 0.25 (6.29–7.14)	6.95 ± 0.19 (6.81–7.08)	7.08, 7.12	5.61
CP4L	2.28	2.52 ± 0.06 (2.40–2.56)	2.82 ± 0.05 (2.78–2.85)	3.04 ± 0.11 (2.84–3.19)	3.25 ± 0.08 (3.16–3.37)	4.19 ± 0.09 (4.12–4.25)	4.05, 4.33	2.74
ML	10.10	10.53 ± 0.18 (10.21–10.78)	11.10 ± 0.13 (10.87–11.32)	12.44 ± 0.34 (11.95–12.89)	13.08 ± 0.37 (12.55–13.62)	15.43 ± 0.45 (15.11–15.74)	16.28, 16.45	11.63
cm3L	5.56	5.74 ± 0.06 (5.62–5.81)	6.04 ± 0.22 (5.88–6.19)	6.69 ± 0.21 (6.30–6.95)	7.07 ± 0.19 (6.81–7.43)	7.84 ± 0.26 (7.65–8.02)	7.83, 8.10	5.91
cp4L	2.18	2.37 ± 0.04 (2.31–2.42)	2.59 ± 0.13 (2.50–2.68)	3.03 ± 0.13 (2.84–3.22)	3.19 ± 0.09 (3.07–3.36)	4.20 ± 0.16 (4.08–4.331)	4.13, 4.24	2.47
CPH	3.47	3.67 ± 0.17 (3.50–4.00)	3.95 ± 0.01 (3.94–3.96)	4.70 ± 0.28 (4.26–5.04)	5.14 ± 0.27 (4.61–5.52)	8.43 ± 0.50 (8.07–8.78)	8.80, 9.66	3.74

Kuo *et al.*, 2009), *M. ryukyuana* (FA mean 36.83, GL 18.65 — Maeda and Matsumura, 1998), *M. shuipuensis* (FA 30.55, GLS 15.90 — Eger and Lim, 2011), and *M. walstoni* (Tables 2 and 4), and slightly larger than *M. suilla* (FA mean 30.70, GTL 14.93 — Hill, 1964; FA mean 30.6, STOTL mean 14.58 — Furey *et al.*, 2009). *Murina kontumensis* sp. nov. also differs from these species in having golden-tipped guard hairs; from *M. shuipuensis* by its plagiopatagium, which attaches to the base of the claw (compared to the base of the toe); from *M. recondita* by its short and bluntly rounded tragus (Fig. 3) (tragus reaches at least half the length of pinna and is sharply pointed in *M. kontumensis* sp. nov.).

Compared with species having predominantly greyish-black pelage, *M. kontumensis* sp. nov. is smaller than *M. beelzebub*, and similar in size to *M. feae* (Tables 2 and 4) and *M. jaintiana* (FA 29.1–31.5, STOTL 14.75–15.25 — Ruedi *et al.*, 2012); *M. kontumensis* sp. nov. has a distinct sagittal crest and developed mesostyles on M2 and M3 (reduced in *M. beelzebub*, *M. jaintiana* and *M. feae*).

The general size of the skull and dentition of *M. kontumensis* (Table 4) is similar to those of *M. chrysochaetes* (Eger and Lim, 2011), *M. harpioloides* (Kruskop and Eger, 2008; IEBR-M5718), *M. eleryi* (Furey *et al.*, 2009), *M. feae* (Thomas, 1891), and *M. walstoni* (Csorba *et al.*, 2011). However, CM3L (Table 4) could be useful to separate *M. kontumensis* from the latter species; *M. kontumensis* sp. nov. (5.01) is larger than *M. aurata* (4.35–4.60 — Maeda, 1980; Furey *et al.*, 2009; Kuo *et al.*, 2009; Csorba *et al.*, 2011), *M. balaensis* (4.66), *M. eleryi* (4.48–4.89), *M. harpioloides* (4.68–4.78), and similar to *M. feae* (4.89–5.38), *M. gracilis* (4.92–5.05 — Kuo *et al.*, 2009), *M. recondita* (4.91–5.10 — Kuo *et al.*, 2009), *M. shuipuensis* (5.23: Eger and Lim, 2011), *M. suilla* (4.54–5.08 — Hill, 1964; Kuo *et al.*, 2009; Csorba *et al.*, 2011), and *M. ussuriensis* (4.95–5.20 — Maeda, 1980), and smaller than *M. walstoni* (6.66–7.14) and *M. beelzebub* (5.47–5.70).

In *M. kontumensis* sp. nov. the ratio of braincase height (BCH) and braincase width (BCW) is 90.8%, whereas all other species of *Murina* from Vietnam, except *M. fionae* and *M. cyclotis*, have ratios less than 90% (Table 4). In comparison of BCH with the other species in Asia, BCH in *M. kontumensis* sp. nov. (6.65) is greater than *M. balaensis* (5.33 — Soisook *et al.*, 2013*a*), *M. tubinaris* (5.55–5.86 — Csorba *et al.*, 2011), *M. pluvialis* (6.43 — Ruedi *et al.*, 2012), and *M. jaintiana* (5.96–6.17 — Ruedi *et al.*, 2012).

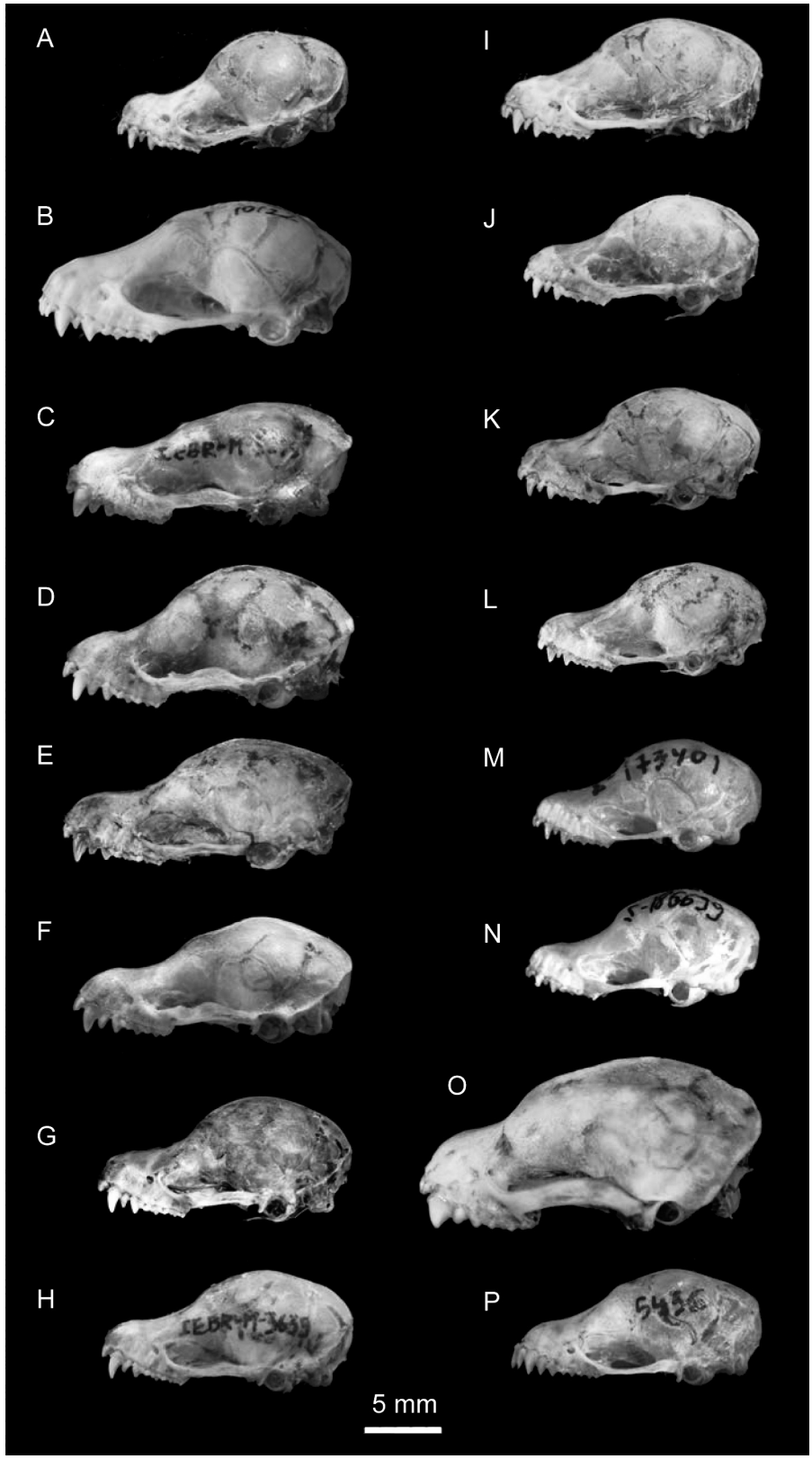

FIG. 5. Left lateral view of skull of specimens from species in the subfamily Murininae in Vietnam: A — *M. kontumensis* sp. nov. (holotype, IEBR-M5697); B — *M. leucogaster* (GZU 10122); C — *M. harrisoni* (IEBR-M3299); D — *M. fionae* (IEBR-M3635); E — *M. huttoni* (IEBR-M5693); F — *M. cyclotis* (IEBR-M4223); G — *M. lorelieae* (IEBR-M5656); H — *M. annamitica* (IEBR-M3639); I — *M. beelzebub* (IEBR-M5645); J — *M. walstoni* (IEBR-VTTu 15-0033); K — *M. feae* (IEBR-M5719); L — *M. eleryi* (IEBR-M5718); M — *M. harpioloides* (ZMMU S173401); N — *M. chrysochaetes* (ZMMU S186699); O — *H. harpia* (IEBR-M422); P — *H. isodon* (IEBR-M5436)

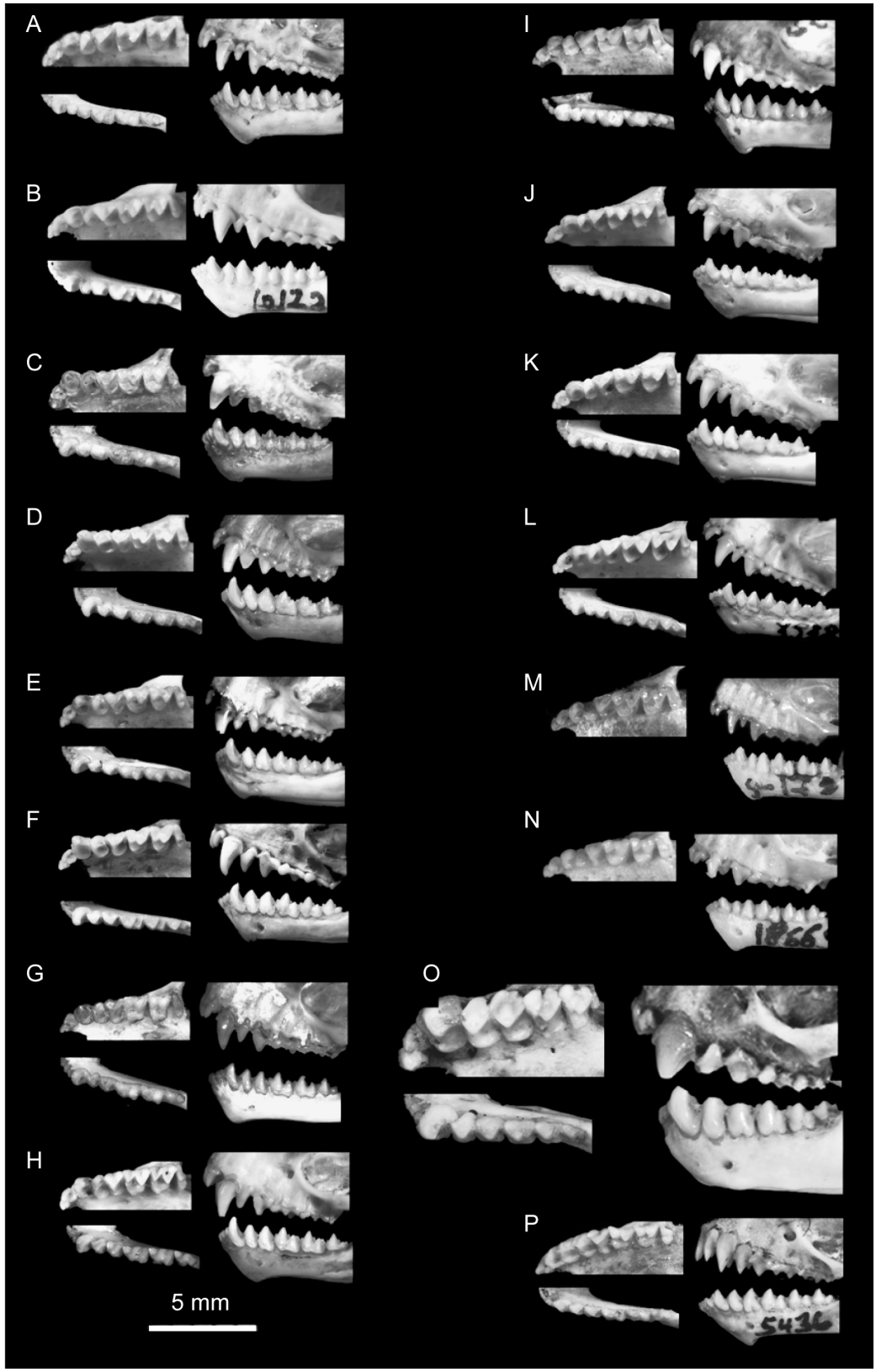

Fig. 6. Lateral and crown view of upper (left) and lower (right) dentition of specimens from species in the subfamily Murininae in Vietnam: A — *M. kontumensis* sp. nov. (holotype, IEBR-M5697); B — *M. leucogaster* (IBHG 10122); C — *M. harrisoni* (IEBR-M3299); D — *M. fionae* (IEBR-M3635); E — *M. huttoni* (IEBR-M5693); F — *M. cyclotis* (IEBR-M4223); G — *M. lorelieae* (IEBR M5656); H — *M. annamitica* (IEBR-M3639); I — *M. beelzebub* (IEBR-M5645); J — *M. walstoni* (IEBR VTTu 15-00033); K — *M. feae* (IEBR-M5719); L — *M. eleryi* (IEBR-M4070); M — *M. harpioloides* (ZMMU S173401); N — *M. chrysochaetes* (ZMMU S186699); O — *H. harpia* (IEBR-M422); P — *H. isodon* (IEBR-M5436)

TABLE 4. Morphological comparison among species of the subfamily Murininae. Sample sizes in parentheses

Species	Sex	STOTL (mm)	CM3L (mm)	ML (mm)	BCH/BCW (%)	IOW/BCW (%)	Dentition	Braincase	Sagittal crest	Lambdoid crest	M1/M2 mesostyles
M. kontumensis sp. nov.	♂	–	–	–	–	–	*suilla*-type	Well domed	Developed	Developed	Well developed
	♀	14.98 (1)	5.61 (1)	10.1 (1)	90.8	53.8					
M. leucogaster	♂	19.27 (1)	6.27 (1)	13.17 (1)	84.7	65.7	*suilla*-type	Domed	Weakly developed	Weak	Weakly developed
	♀	18.49 (1)	6.33 (1)	13.32 (1)	80.8	61.1					
M. harrisoni	♂	16.95–18.39 (12)	5.82–6.31 (12)	11.95–12.89 (12)	77.9–89.1	53.5–58.3	*cyclotis*-type	Flat	Well developed	Well developed	Weakly developed
	♀	17.46–19.72 (11)	6.29–7.14 (11)	12.55-13.75 (11)	79.0–92.9	54.2–58.6					
M. fionae	♂	17.86–18.23 (6)	6.10–6.38 (6)	12.05–12.44 (6)	84.1–94.4	54.3–58.3	*cyclotis*-type	Well domed	Well developed	Weakly developed	Absent
	♀	19.08 (1)	6.39 (1)	12.85 (1)	91.5	57.0					
M. huttoni	♂	16.61–18.52 (14)	5.56–6.23 (14)	11.35–12.30 (14)	80.1–93.1	54.7–60.3	*cyclotis*-type	Flat	Weakly developed	Weakly developed	Well developed
	♀	16.61–18.81 (14)	5.66–6.30 (14)	11.59–12.70 (14)	79.8–87.9	55.0–59.6					
M. cyclotis	♂	16.08–17.66 (40)	5.16–5.59 (40)	10.44–11.87	77.7–96.2	51.7–57.8	*cyclotis*-type	Domed	Weakly developed	Weakly developed	Absent
	♀	16.70–18.08 (33)	5.55–5.89 (33)	10.90–12.34 (33)	80.5–96.4	51.7–58.3					
M. lorelieae	♂	15.83–16.39 (7)	5.21–5.40 (7)	10.21–10.78 (7)	86.8–94.1	55.5–57.0	*suilla*-type	Domed	Absent	Weak	Well developed
	♀	16.33–16.74 (3)	5.46–5.64 (3)	10.79–11.32 (3)	82.8–89.8	55.6–57.8					
M. annamitica	♂	15.63–16.47 (11)	5.19–5.60 (11)	10.13–10.98 (11)	82.4–91.6	53.6–58.9	*cyclotis*-type	Domed	Weakly developed	Weak	Well developed
	♀	16.40–17.16 (11)	5.23–5.69 (11)	10.69–11.47 (11)	80.5–90.5	54.8–60.5					
M. beelzebub	♂	16.40–16.69 (4)	5.27–5.54 (4)	10.73–11.11 (4)	80.8–83.3	56.5–59.0	*suilla*-type	Domed	Absent	Weak	Weakly developed
	♀	16.73–16.99 (6)	5.40–5.70 (6)	10.88–11.48 (6)	79.8–83.7	59.0–61.1					
M. walstoni	♂	15.39–15.73 (3)	5.34–5.39 (3)	10.62–10.74 (3)	79.3–90.9	54.7–57.0	*suilla*-type	Domed	Well developed	Well developed	Developed
	♀	15.15–15.92 (6)	5.27–5.48 (6)	10.40–10.95 (6)	86.1–94.5	56.7–62.6					
M. feae	♂	14.91–16.30 (20)	4.62–5.25 (20)	9.63–10.64 (20)	76.4–91.1	53.6–62.0	*suilla*-type	Domed	Absent	Weak	Weak
	♀	15.13–16.11 (18)	4.89–5.47 (18)	9.80–10.86 (18)	76.4–88.0	55.2–63.3					
M. eleryi	♂	13.79–15.18 (9)	4.53–4.79 (8)	9.25–9.60 (8)	79.5–84.2	56.7–62.6	*suilla*-type	Domed	Absent	Weak	Well developed
	♀	14.21–15.15 (10)	4.48–4.89 (10)	9.28–9.97 (10)	76.6–87.8	58.4–60.7					
M. harpioloides	♂	14.62 (1)	4.70 (1)	9.52 (1)	90.3	58.6	*suilla*-type	Domed	Absent	Weak	Weak
	♀	14.53 (1)	4.68 (1)	9.31 (1)	88.2	57.0					
M. chrysochaetes	♂	–	–	–	–	–	*suilla*-type	Domed	Absent	Weak	Reduced
	♀	14,57, 14.72 (2)	4.66, 5.44 (2)	9.30, 9.94 (2)	87.0, 89.0 (2)	57.3, 59.5					
H. harpia	♂	21.45, 23.07 (2)	6.81, 7.09 (2)	15.11, 15.74(2)	100.8, 101.0	59.0, 59.2	–	Domed	Well developed	Well developed	Absent
	♀	22.82–23.25 (3)	7.08–7.12 (3)	16.28–16.45 (3)	97.6, 105.4	55.8, 59.6					
H. isodon	♂	–	–	–	–	–	–	Domed	Absent	Weakly developed	Weak
	♀	17.09 (1)	5.61 (1)	11.63 (1)	100.6	66.3					

The ratio of interorbital width to braincase width (IOW:BCW) for *M. kontumensis* sp. nov. was 53.8%, while other *Murina* species, except *M. cyclotis*, had more than 54% (Table 4). This is related to the narrower nasal sinus of *M. kontumensis* sp. nov. than that in the other *Murina* species.

Karyotype

Karyotype (Fig. 7A and Table 5) of the holotype was 2n = 44, FN = 50. Autosomes consisted of three large metacentric pairs, one small submetacentric pair, and 17 medium-sized to small acrocentric pairs, gradually decreasing in size. The X chromosome was identified as a large submetacentric element.

Distribution and ecological notes

Holotype was collected by mist nets set along a stream in relatively undisturbed primary forest at 1,780 m a.s.l. The nearby Ngoc Linh Mountain (ca. 2,598 m a.s.l.) is situated at the northwestern margin of Kon Tum province, and is the highest point of the Truong Son (Annamite) Range in Central Highlands of Vietnam. The primary vegetation at the collection site was moist evergreen forest, with a mixture of abundant bananas and bamboos on the slopes.

Ngoc Linh is split into two nature reserves: one in Quang Nam Province and another in Kon Tum Province. Ngoc Linh (Kon Tum) Nature Reserve was established in 1986 for the conservation of the evergreen forest and covers 41,240 ha in Dak Glei and Dac To districts. This part of the Central Highlands includes a complex mosaic of volcanic basalts, granites and sedimentary substrates with wet evergreen hardwood and conifer forests. A total of 55 mammal species were recorded for Ngoc Linh (Kon Tum) Nature Reserve (Trai *et al.*,

FIG. 7. Karyotypes of specimens from species in the subfamily Murininae from Vietnam: A — *M. kontumensis* sp. nov. (holotype, IEBR-M5697); B — *M. huttoni* (IEBR-M5407); C — *M. cyclotis* (IEBR-M4071); D — *M. lorelieae* (HNHM B20140915.7); E —*M. beelzebub* (IEBR-M4842); F — *M. feae* (IEBR-M4214); G — *H. harpia* (IEBR-M5661); H — *H. isodon* (IEBR-M5436)

1999, 2000; Tordoff *et al.*, 2000; Abramov *et al.*, 2006).

Murina leucogaster Milne-Edwards, 1872

Murina leucogaster Milne-Edwards, 1872: 252; Type locality: Moupin, Sichuan, China.
Murina leucogaster: Hendrichsen *et al.*, 2001: 102.

Distribution

Northeast India, Nepal, western Thailand, Vietnam, and southern China (Milne-Edwards, 1872; Tate, 1941; Hill, 1964; Corbet and Hill, 1992; Bates and Harrison, 1997; Hendrichsen *et al.*, 2001; Simmons, 2005; Smith and Xie, 2008). In Vietnam (Fig. 1): Nghe An (Pu Mat NP) [22] (Hendrichsen *et al.*, 2001).

Diagnostic descriptions

Large species with '*suilla*-type' dentition (Table 4). Wing membranes are greyish-brown, the muzzle is dark, and the ears are relatively narrow and short. There is a basal notch in the outer margin of ears. Pelage is thick and woolly, with hairs covering the interfemoral membrane and toes. The dorsum is ferruginous red with dark brown roots; ventrum is pale yellow with dark grey roots on the flanks. Wing is attached at the base of the toe claw and the tail is hairy.

Skull and dentition (Figs. 5 and 6). Rostrum is not inflated and the braincase is domed. Sagittal and lambdoid crests are relatively weak. I2 is partly anterior to I3. C is slightly higher than or subequal to P4. C basal area is smaller than that of P4. P2 is small with a basal area one-third that of P4. M1 and M2 mesostyles are weakly developed. In the mandible, talonids on the lower molars are smaller than the corresponding trigonids. We measured a female skull (HZM 1.31758) from Vietnam and a male skull (IBHG 10122) from Sichuan Province, China (Table 4).

Taxonomic note

Milne-Edwards (1871) originally described *M. leucogaster* from Moupin, Szechwan, China. In Vietnam, Hendrichsen *et al.* (2001) only recorded one specimen from Pu Mat National Park, Nghe An Province and no further specimens were found.

Murina harrisoni Csorba and Bates, 2005

Murina huttoni: Hendrichsen *et al.*, 2001: 103 (part).
Murina harrisoni Csorba and Bates, 2005: 2; Type locality: O Tuk Chehn, Kirirom National Park, Kompong Speu Province, Cambodia; Wu *et al.*, 2010: 277; Francis and Eger, 2012: 29; Thomas *et al.*, 2013: 231.
Murina tiensa Csorba, Thong, Bates and Furey, 2007: 3; Type locality: An Tinh commune, Na Ri district of Kim Hy Nature Reserve, Bac Kan Province, Vietnam, about 750 m a.s.l.

Distribution

Vietnam, Laos, Cambodia, Myanmar, Thailand, southern China including Hainan Island (Csorba and Bates, 2005; Csorba *et al.*, 2007; Wu *et al.*, 2010; Francis and Eger, 2012).

In Vietnam (Fig. 1): Son La (Co Ma and Thuan Chau district) [13], Phu Tho (Xuan Son NP) [12], Bac Kan (Kim Hy NR) [6], Hai Phong (Cat Ba NP) [10], Vinh Phuc (Tam Dao NP) [11], Thanh Hoa (Xuan Lien) [19], Nghe An (Pu Mat NP) [22], Dak Lak (Yok Don NP) [34] (This study; Csorba *et al.*, 2007; Thong *et al.*, 2011; Francis and Eger, 2012).

Description

Large species with '*cyclotis*-type' dentition (Fig. 4, Tables 2, 3, and 4). The ear is round and large. The hairs of the dorsal fur are pale-based, light, yellowish-red, gradually darkening towards the tip. The ventral pelage is uncoloured whitish or light grey. Plagiopatagium attached to the base of the toe claw.

Skull and dentition (Figs. 5 and 6). Rostrum not inflated and the braincase is flat. Sagittal and lambdoid crests are well developed. I2 is lateral to I3. C is much higher than P4. C basal area equals or slightly larger than that of P4. P2 height is subequal to P4; its basal area is two-third or almost equals that of P4. M1 and M2 mesostyles are weakly developed. Lower canines are well developed. The height of p2 is about equal to that of the p4; m1 and m2 have well-developed talonids, and have a well-defined hypoconids and entoconids.

Taxonomic note

Csorba and Bates (2005) described *M. harrisoni* as a new species from Cambodia. Subsequently, Csorba *et al.* (2007) described another species, *M. tiensa* from Vietnam, and mentioned that *M. tiensa* differs from *M. harrisoni* by the insertion point of the wing membrane, and rostral characteristics where the anterior part of the rostrum is almost straight in *M. tiensa*, and more bulbous in *M. harrisoni*. Francis and Eger (2012) regarded *M. tiensa* as a junior synonym of *M. harrisoni* in examining specimens from Laos, Thailand, China and Vietnam, and concluded that the morphological characteristics separating the two species were actually intraspecies variation. DNA sequence variation among these specimens indicated two distinct clades, but the divergence of all specimens was less than 5–6%.

TABLE 5. Comparison of karyotypes of the subfamily Murininae. Abbreviations: M: metacentrics; SM: submetacentrics; ST: mubtelocentrics; A: acrocentrics

Species	Locality	2n	FN	M	SM	ST	A	X	Y	References
M. kontumensis sp. nov.	Vietnam	44	50	3	1	0	17	M	–	This study (n = 1)
M. leucogaster	China	44	58	3	1	4	13	M	A	Gu (2006)
M. hilgendorfi	Japan	44	56	3	1	3	14	SM	A	Harada (1973), Ando *et al.* (1977), Harada *et al.* (1987)
M. harrisoni	China	44	50	3	1	0	17	M	–	Wu *et al.* (2010)
M. harrisoni	Thailand	44	50	3	1	0	17	M	A	McBee *et al.* (1986), see also Francis and Eger (2012)
M. huttoni	Vietnam	44	50	3	1	0	17	M	A	This study (n = 5)
M. cyclotis	Vietnam	44	50	3	1	0	17	M	A	This study (n = 5)
M. lorelieae	Vietnam	44	50	3	1	0	17	SM	A	This study (n = 2)
M. beelzebub	Vietnam	44	50	3	1	0	17	M	–	This study (n = 1)
M. feae	Vietnam	44	50	3	1	0	17	M	–	This study (n = 1)
M. feae	China	44	50	3	1	0	17	M	A	Zhou *et al.* (2011)
M. puta	Taiwan	44	50	3	1	0	17	M	A	Lin *et al.* (2002)
M. suilla	Malaysia	44	58	3	1	4	13	SM	ST	Volleth (2006)
M. ussuriensis	Japan	44	56	3	0	4	14	M	A	Ono and Obara (1994)
M. ussuriensis	Japan	44	56	3	1	3	14	SM	A	Ando *et al.* (1977), Harada *et al.* (1987)
H. harpia	Vietnam	44	52	4	1	0	16	M	A	This study (n = 1)
H. harpia	Taiwan	44	52	4	1	0	16	M	–	Lin *et al.* (2006)
H. harpia	China	44	52	4	1	0	16	M	A	Zhou *et al.* (2014)
H. harpia	Thailand	40	–	–	–	–	–	–	–	McBee *et al.* (1986)
H. isodon	Vietnam	44	50	3	1	0	17	M	–	This study (n = 1)

Thereafter, Wu *et al.* (2010) reported the species as *M. harrisoni* from Hainan Island, China, and Son *et al.* (2015) recognized *M. tiensa* instead of *M. harrisoni* for specimens from Vietnam.

To clarify the relationship between *M. harrisoni* and *M. tiensa*, we examined specimens from the collections of HZM, HNHM, IEBR, ROM, and IBHG. Plots between size PC1 (PCA of log-transformed raw data) and shape PC1 (PCA of log-transformed standardized data) are given in Fig. 8. In size PC1, females were larger than males with little overlap. Size PC1 and shape PC1 (based on log-transformed standardized data) had a negative correlation. Size PC1 explained 76.2% of the variance, and all characters had positive loading factors between 0.090–0.459. The shape PC1 explained 33.6% of the variance, and CPH (-0.586, negative), BCW (0.472, positive), and IOW (0.442, positive) showed high factor loadings. Holotypes of *M. harrisoni* and *M. tiensa* (both females) plotted closely. This result does not support the existence of two distinct species. We, therefore, suggest that the observed morphological variation is intraspecific variation found in *M. harrisoni* and involves strong sexual dimorphism; consequently, we regard *M. tiensa* as a junior synonym of *M. harrisoni*. Because the number of specimens was not sufficient at each locality, we cannot provide conclusions about geographic variation and the possible intraspecific divergence within *M. harrisoni*.

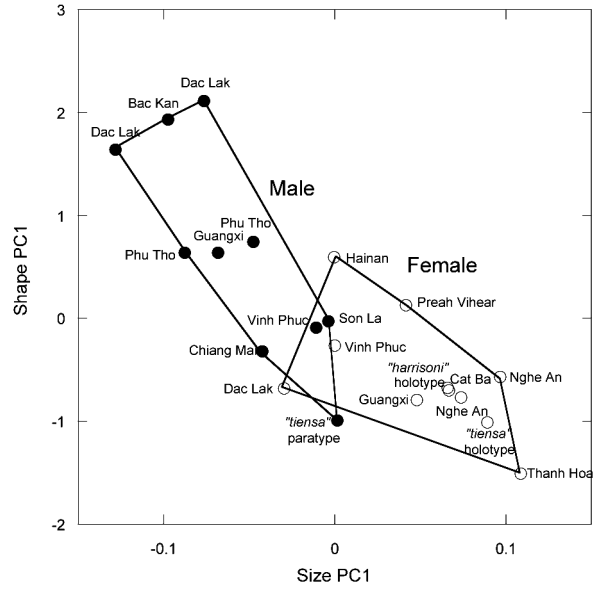

FIG. 8. Scatter plots between size PC1 and shape PC1 based on craniodental measurements of *M. harrisoni* and '*M. tiensa*' specimens. Open and closed circles represent females and males, respectively

Difference in the braincase region between males and females was relatively small, as shown in the area connecting the posterior end of the interorbital region, outer margin of the braincase and the posterior end of the skull in dorsal view (Fig. 9). On the other hand, the area of the nasal capsule was expanded more laterally and anteriorly in females than males, with a line connecting the anterior end of the interorbital region, the anterior of the zygomata, the posterior margin of the canines, and the anterior tip of the skull. In addition, females have well-developed canines (C) and a robust rostrum as compared to males (Fig. 9).

Size and shape of the braincase and nasal capsule may be related to functional limitation for size and shape change throughout various regions. Therefore, sexual dimorphism is suggested to have achieved under these functional limitations different among skull regions (e.g., braincase and nasal capsule), and not necessarily with simple overall size change and accompanied allometric shape changes. As a result, sexual dimorphoism is to become so complicated pattern. Previously observed profile variation in *M. harrisoni* and *M. tiensa* should be re-evaluated with consideration of these complicated morphological variations among the sexes (Fig. 9). In addition, the difference in length of the interorbital region (elongated in females) likely results in a difference in bite force between sexes. To understand the sexual dimorphism, three-dimensional geometric morphometric or CT scanning reconstruction methods are needed.

Francis and Eger (2012: Fig. 9) provided photos of five individuals of *M. harrisoni* and *M. tiensa*. The smallest depicted female specimen (HZM 1.31525) has caused confusion, suggesting that females and males widely overlap in overall size. Our STOTL measurement of the same specimen (19.33 mm), however, is actually closer to the two larger female specimens, EGD 24974 (19.87 mm) and HZM 1.36316 (18.39 mm; erroneously labelled as '1.36136' in the caption). We assume that scaling or size adjustment error must have occurred during the preparation of the figure in Francis and Eger (2012).

Murina fionae Francis and Eger, 2012

Murina CMF sp. B: Francis *et al.*, 2010: 6.

Murina peninsularis: Matveev and Csorba, 2007: 100.

Murina fionae Francis and Eger, 2012: 32; Type locality: Pha Deng, 8 km E of Ban Navang, Khammouan Province, Laos, 1,140 m a.s.l.; Thomas *et al.*, 2013: 231.

Distribution

Vietnam, Laos, and Cambodia (Francis and Eger, 2012; Soisook *et al.*, 2013*b*).

In Vietnam (Fig. 1): Quang Binh (Phong Nha-Ke Bang NP) [24], Quang Tri (Bac Huong Hoa NR)

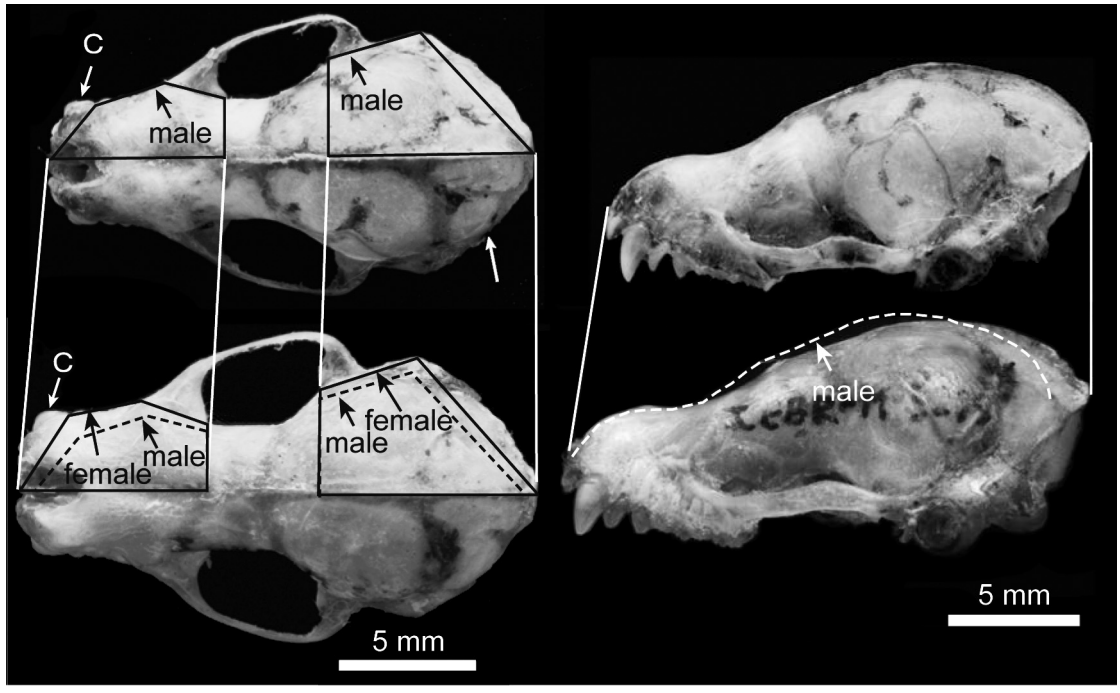

FIG. 9. Dorsal and left lateral views of skulls from male (B190913.7, top) and female (PM28, bottom) specimens of *M. harrisoni*

[25], Quang Nam (Ngoc Linh NR, Song Thanh NR) [27, 28], Quang Ngai (Ba To area) [30], Kon Tum (Chu Mom Ray NP) [31], Gia Lai (Kon Cha Rang NR, Kon Ka Kinh NP) [32], Dong Nai (Cat Tien NP) [39] (This study; Francis and Eger, 2012; Soisook *et al.*, 2013*b*).

Description

Large species with '*cyclotis*-type' dentition (Fig. 4, Tables 2 and 4). Ears are moderately large and rounded. The fur of the dorsum is long with pale buff bases and orange-brown tips. Scattered longer guard hairs are pale to the tip, creating a frosted appearance. The hairs of the ventrum are unicoloured, pale buff orange over most of the venter, but more whitish near the chin. The interfemoral membrane, legs, feet and tail are covered with long orange-brown hairs, which are relatively dense on the legs and feet. Plagiopatagium is attached to the base of the toe claw.

Skull and dentition (Figs. 5 and 6). Rostrum is not inflated and the braincase is well domed. Sagittal crest is strong and the lambdoid crest is weakly developed. I2 is lateral to I3, C is much higher than P4. C basal area is slightly larger or equal to P4. P2 height is subequal to P4, its basal area is two-thirds to nearly equal to P4. No mesostyles are on M1 and M2. In the mandible, talonids of m1 and m2 are reduced relative to trigonid. In the lateral view, posterior cusps are slightly more than half the height of the anterior cusps. When viewing from above, the length of the talonid is less than half the length of trigonid.

Taxonomic note

Francis and Eger (2012) described this species based on specimens from Laos and Vietnam.

Murina huttoni (Peters, 1872)

Harpiocephalus huttoni Peters, 1872: 257; Type locality: Dehra Dun, Kumaon, northwestern India.

Murina huttoni: Hendrichsen *et al.*, 2001: 103; Francis and Eger, 2012: 20; Thomas *et al.*, 2013: 231.

Distribution

Northwest India, Tibet to Thailand, Vietnam, northeastern and southern China, and west Malaysia (Tate, 1941; Hill, 1964; Corbet and Hill, 1992; Bates and Harrison, 1997; Simmons, 2005; Smith and Xie, 2008; Zhou *et al.*, 2011).

In Vietnam (Fig. 1): Lao Cai (Hoang Lien NP) [1], Cao Bang (Phia Oac-Phia Den NR) [5], Nghe An (Pu Mat NP) [22], Quang Tri (Bac Huong Hoa NR) [25], Quang Nam (Ngoc Linh NR) [28], Kon Tum (Ngoc Linh NR) [29], Dak Lak (Chu Yang Sin NP) [35], Lam Dong (Bi Dup-Nui Ba NP) [36], Khanh Hoa (Hon Ba NR) [37] (This study; Can *et al.*, 2008; Kruskop, 2013).

Description

Medium-sized species with '*cyclotis*-type' dentition (Fig. 4, Tables 2 and 4). Both dorsum and ventral fur are dark. The fur of the dorsum is long and fluffy, and is slate grey with a pale buffy band which darkens gradually into a darker orange-brown band. The ventral fur is similar but somewhat paler. The interfemoral membrane is extensively covered with reddish-brown hairs, which are longer near the body and shorter near the edge. Plagiopatagium is attached to base of the toe claw.

Skull and dentition (Figs. 5 and 6). Rostrum is not inflated and the braincase is flat. Sagittal and lambdoid crests are weakly developed. I2 is lateral or partly anterior to I3. C is much higher than P4. C basal area equals that of P4. P2 height is subequal to P4, and its basal area is two-thirds that of P4. M1 and M2 mesostyles are well developed. In the mandible, talonids of m1 and m2 are well developed; viewed from above, the length of talonids on the lingual side is only slightly less than that of trigonid; in lateral view, the posterior cusps are about two-thirds the height of the anterior cusps.

Karyotype

Karyotype (Fig. 7B and Table 5) was 2n = 44, FN = 50. Autosomes consisted of three large metacentric pairs, one small submetacentric pair, and 17 medium-sized to small acrocentric pairs that gradually decrease in size. The X chromosome pair could be identified as a medium-sized metacentric element.

Taxonomic note

Hill (1964) and Corbet and Hill (1992) recognised two subspecies: *M. huttoni rubella* (Thomas, 1914) (from southeast China and probably in north Thailand) and *M. h. huttoni* (Peters, 1872) (from the rest of the area) in having different colour patterns. In Vietnam, we found variation in colour among two specimens from Hoang Lien National Park (Lao Cai province): a more reddish orange specimen that is most similar to *M. huttoni rubella* (Hill, 1964; Hendrichsen *et al.*, 2001; Francis and Eger, 2012), and a more greyish brown individual in concordance with the description of *M. h. huttoni*. Additional studies covering the whole distribution range are needed to understand the possible cryptic diversity.

Murina cyclotis Dobson, 1872

Murina cyclotis Dobson, 1872: 210; Type locality: Darjeeling, NE India; Hendrichsen *et al.*, 2001: 104; Ith *et al.*, 2011: 97; Francis and Eger, 2012: 17; Thomas *et al.*, 2013: 230; Soisook *et al.*, 2013*b*: 274.

Distribution

Sri Lanka, India, Myanmar, Laos, Vietnam, southern China in Guangdong Province and Hainan Island, south to West Malaysia, Borneo, Sumatra, Philippines, and Lesser Sunda (Tate, 1941; Ellerman and Morrison-Scott, 1951; Hill, 1964; Corbet and Hill, 1992; Bates and Harrison, 1997; Francis *et al.*, 1999; Simmons, 2005; Francis, 2008; Smith and Xie, 2008; Ith *et al.*, 2011; Francis and Eger, 2012; Soisook *et al.*, 2013*b;* Thomas *et al.*, 2013).

In Vietnam (Fig. 1): Son La (Xuan Nha NR) [15], Phu Tho (Xuan Son NP) [12], Cao Bang (Phia Oac-Phia Den NR) [5], Vinh Phuc (Tam Dao NP) [11], Quang Ninh (Bai Tu Long NP) [9], Hai Phong (Cat Ba NP) [10], Ninh Binh (Cuc Phuong NP) [18], Thanh Hoa (Pu Hu NR, Pu Luong NR, and Xuan Lien NR) [16, 17, 19], Nghe An (Pu Huong NR, Pu Mat NP) [21, 22], Quang Binh (Phong Nha-Ke Bang NP) [24], Quang Tri (Dakrong NR) [25], Thua Thien-Hue (Bach Ma NP) [26], Kon Tum (Ngoc Linh NR) [29], Quang Ngai (Ba To area) [30], Gia Lai (Kon Ka Kinh NP) [32], Binh Dinh (Phu Yen district) [33], Lam Dong [36], Binh Phuoc [41], Ba Ria-Vung Tau [42] (This study; Can *et al.*, 2008; Kruskop, 2013).

Description

Medium-sized species with '*cyclotis*-type' dentition (Fig. 4, Tables 2 and 4). The ears are relatively long. The hairs of the dorsum have grey to dark grey bases, and a buffy area that gradually darkens to orange near the tips, but does not create strongly contrasting bands of colour. The hairs on the ventral surface have dark grey bases with buffy white tips, which may have a slight orange colouration. However, orange covers most of the venter, and is more whitish near the tips for specimens in the south. Plagiopatagium is attached to the base of the toe claw.

Skull and dentition (Figs. 5 and 6). Rostrum not inflated and the braincase is slightly domed in females, and more domed in males. Sagittal and lambdoid crests are weak. I2 is lateral to I3, but I3 partly anterior to I2. C is much higher than P4. The C basal area is equal or is slightly larger than P4. P2 height is subequal to or slightly shorter than P4, and its basal area is two-third that of P4. No mesostyle is found on M1 and M2. In the mandible, the talonid of m1 and m2 is greatly reduced relative to the trigonid. Viewed from above, the length of the talonid is less than half the length of the trigonid. In the lateral view, the posterior cusps are no more than half the height of the anterior cusps. In the mandible, both premolars are similar in height.

Karyotype

Karyotype (Fig. 7C and Table 5) was 2n = 44, FN = 50. Autosomes consisted of three large metacentric pairs, one small submetacentric pair, and 17 medium-sized to small acrocentric pairs that gradually decrease in size. The X chromosome was a medium-sized metacentric element, and the Y chromosome was a small acrocentric element.

Taxonomic note

Ellerman and Morrison-Scott (1951), Hill (1964), Eisenberg and McKay (1970), Corbet and Hill (1992), Koopman (1994), Simmons (2005) recognized three subspecies: *M. cyclotis eileenae* (Ceylon), *M. cyclotis cyclotis* (Northeastern India to Hainan and Vietnam), and *M. cyclotis peninsularis* (Malaysia). Francis and Eger (2012) elevated *M. peninsularis* to full species, and suggested that *M. cyclotis* sensu stricto is a complex of cryptic taxa; therefore, future taxonomic studies covering its wide distribution are desired. Soisook *et al.* (2013*b*) studied this species' complex and considered *eileenae* to be a synonym of *M. cyclotis*, and *M. peninsularis* to be a valid species. In addition, Soisook *et al.* (2013*b*) described a new species, *M. guilleni,* from Thailand and further discussed the taxonomic problems in *M. cyclotis* that should be addressed in future studies.

Murina lorelieae Eger and Lim, 2011

Murina lorelieae Eger and Lim, 2011: 234; Type locality: Diding Headwater Forest Nature Reserve, Jing Xi County, Guangxi Zhuang Autonomous Region, China.

Murina lorelieae ngoclinhensis Tu, Cornette, Utge and Hassanin, 2015: 209; Type locality: Ngoc Linh Nature Reserve, Vietnam.

Distribution

Southern China, Vietnam (Tu *et al.*, 2015).

In Vietnam (Fig. 1): Kon Tum (Ngoc Linh NR) [29] (This study; Tu *et al.*, 2015).

Description

Medium-sized species with '*suilla*-type' dentition (Fig. 4, Tables 2, 3, and 4). The ear is round and

both sides of the muzzle are dark brown. The pelage is characterized by long shiny hairs (8 mm ventrally and 13–15 mm dorsally), with distinct copper reddish-brown and dirty white colourations on dorsal and ventral surfaces. Dorsal hairs are dark grey basally, pale in the middle and reddish brown at the tip. Ventral hairs are dark grey to about two-thirds of the length and whitish at the tip.

Skull and dentition (Figs. 5 and 6). The skull is domed. The lateral profile of the anterior part of the skull gradually rises from the rostrum to the forehead. The sagittal crest is lacking; lambdoid crest is visible but very weak. Maxillary toothrows are convergent anteriorly. The dentition is quite robust. I2 is anterior to I3, and I2 is visible laterally. I2 and I3 are subequal in height and are much less than half the height of upper C. Upper C slightly but clearly exceeds the height of P4, the basal area of C is less than that of P4. The crown area of P2 is slightly more than half that of P4. M1 and M2 have well developed mesostyles and curved labial faces. Paracone, metacone, and protocone of M1 and M2 are distinctly defined.

Karyotype

Karyotype (Fig. 7D and Table 5) based on a specimen from Kon Tum province (Ngoc Linh Nature Reserve) was 2n = 44, FN = 50. Autosomes consisted of three large metacentric pairs, one small submetacentric pair, and 17 medium-sized to small acrocentric pairs that gradually decrease in size. The X chromosome was a medium-sized submetacentric, and the Y chromosome was a small acrocentric element.

Taxonomic note

Eger and Lim (2011) described *M. lorelieae* based on a single specimen from Diding Headwater Forest Nature Reserve, Jing Xi County, Guangxi Zhuang Autonomous Region, China; close to the border with northeast Vietnam. Tu *et al.* (2015) recorded this species from Ngoc Linh Mountain in the Central Highlands of Vietnam at over 1,600 m elevation (Tu *et al.*, 2015). Based on DNA barcoding and morphological data, Tu *et al.* (2015) described a new subspecies *M. lorelieae ngoclinhensis*. This species has been recorded only from two localities at high elevations in southern China and Vietnam, but additional surveys are expected to find new localities and to further describe the geographic boundary of the two subspecies. Although Tu *et al.* (2015) regarded *M. lorelieae* as a member of the *M. cyclotis*-group (on the basis of three specimens from Vietnam), a closer examination of additional specimens proved that *M. lorelieae* shows '*suilla*-type' dentition.

Murina annamitica Francis and Eger, 2012

Murina CMF sp. D: Francis *et al.*, 2010: 6.

Murina annamitica Francis and Eger, 2012: Type locality: near Nam Pan in the Annamite Mountains, Bolikhamxai Province, Laos, about 1,300 m a.s.l.; Thomas *et al.*, 2013: 231.

Distribution

Vietnam and Laos (Francis and Eger, 2012).

In Vietnam (Fig. 1): Son La (Xuan Nha NR) [15], Lao Cai (Hoang Lien NP) [1], Tuyen Quang (Na Hang NR) [3], Thanh Hoa (Pu Luong NR) [17], Nghe An (Pu Huong NR and Pu Mat NP) [22], Quang Tri (Bac Huong Hoa NR) [25], Quang Nam (Ngoc Linh) [28], Kon Tum (Ngoc Linh) [29], Quang Ngai (Ba To area) [30], Binh Phuoc (Bu Gia Map NR) [41] (This study; Francis and Eger, 2012; Kruskop, 2013).

Description

Medium-sized species with '*cyclotis*-type' dentition (Fig. 4, Tables 2 and 4). The interfemoral membrane is extensively covered with hairs. There are very short hairs on the forearm and leading edge of the wing. Plagiopatagium is attached to the base of the toe claw. The ear is round without a notch on its posterior border. Dark bases extend to the fur of the dorsum. The fur of the dorsum is long and fluffy. The hairs have slate grey bases followed by a buffy band, then darker brown to orange-brown tips. The overall appearance is orange-brown to brown. The fur of the underside has slate grey bases followed by buffy tips, giving an overall greyish buff appearance.

Skull and dentition (Figs. 5 and 6). Rostrum not inflated and the braincase is domed. Sagittal and lambdoid crests are weak. I2 is lateral to I3. C basal area equals that of P4. P2 is less in height than P4 and its basal area is two-thirds that of P4. M1 and M2 mesostyles are well developed, comparable in height to the metastyle and parastyle, giving a distinct W-shape to the surface. In the mandible, both premolars are similar in height, and lower molars have well-developed talonids.

Taxonomic note

Francis and Eger (2012) described *M. annamitica* as a new species from Laos; and also referred material from the centre of Vietnam.

Murina beelzebub Son, Furey and Csorba 2011

Murina tubinaris: Hendrichsen *et al.* 2001: 103 (part).

Murina beelzebub Son, Furey and Csorba, 2011 in Csorba *et al.*, 2011: 899; Type locality: Bac Huong Hoa Nature Reserve, Huong Hoa District, Quang Tri Province, Vietnam, 400 m a.s.l.

Distribution

Recorded only from Vietnam. In Vietnam (Fig. 1): Quang Tri (Bac Huong Hoa NR) [25], Kon Tum (Ngoc Linh NR) [29], Quang Ngai (Ba To area) [30], Gia Lai (Kon Ka Kinh NP) [32] (This study; Csorba *et al.*, 2011).

Description

Medium-sized species with '*suilla*-type' dentition (Fig. 4, Tables 2 and 4). On the dorsal surface, the proximal sixth of individual hairs is very dark brown (almost black), whereas the remaining distal portion is initially light grey and terminates in a distinctly darker tip. Longer silver guard hairs are scattered over all of the dorsum. The upper surface of the hind limbs, feet, and uropatagium are densely covered in long, uniformly dark brown hairs. Ventrally, hairs are very dark brown (almost black) for the proximal two-thirds, whereas the remaining upper portion is white. Ventral surface of the uropatagium is covered in uniformly white hairs, some of which are also present on the plagiopatagium adjacent to the body. The ear has a slight emargination along its posterior border, and the plagiopatagium is attached to the base of the claw on the outer toe.

Skull and dentition (Figs. 5 and 6). Rostrum is not inflated and the braincase is domed. No sagittal crest, and the lambdoid crest is weak. Rostrum is slightly elongated but is not inflated. The depth of the narial emargination exceeds its width. The zygoma is strong and possesses a slight dorsal process. A medial process is present in the posterior palatal region. The medial ridge separating the basioccipital pits is relatively narrow, and the anterior borders of the pits are weakly defined. I2 is partly anterior to I3. C is slightly higher than P4. C has a basal area smaller than that of P4. P2 is much shorter than P4; its basal area is half that of P4. M1 and M2 mesostyles are weakly developed. In the mandible, p2 has less than one-half the basal area of p4 and attains more than two-thirds its height. Talonids of m1 and m2 equal their trigonids in the crown area and entoconids of the teeth distinctly exceed their hypoconids in height.

Karyotype

Karyotype (Fig. 7E and Table 5) based on a female specimen from Quang Tri province (Bac Huong Hoa Nature Reserve) was 2n = 44, FN = 50. Autosomes consisted of three large metacentric pairs, one small submetacentric pair, and 17 medium-sized to small acrocentric pairs that gradually decrease in size. The X chromosome pair could be identified as a medium-sized submetacentric element.

Taxonomic note

The first specimen (HZM) was collected around Kon Cha Rang and Kon Ka Kinh Nature Reserve (1,600 m a.s.l.) by Benjamin Hayes (Trai *et al.*, 2000), which Hendrichsen *et al.* (2001) identified as *M. tubinaris*. Thereafter, Csorba *et al.* (2011) described *M. beelzebub* based on specimens from central Vietnam (Quang Tri province) and the HZM specimen from Kon Ka Kinh Nature Reserve.

Murina walstoni Furey, Csorba and Son, 2011

Murina walstoni Furey, Csorba and Son, 2011 in Csorba *et al.*, 2011: 900; Type locality: Veun Sai Protected Forest, Veun Sai District, Cambodia, 110 m a.s.l.; Francis and Eger, 2012: 29; Thomas *et al.*, 2013: 232.

Distribution

Vietnam, Laos, and Cambodia (Csorba *et al.*, 2011; Francis and Eger, 2012; Kruskop, 2013; Thomas *et al.*, 2013). In Vietnam (Fig. 1): Dak Lak (Yok Don NP) [34], Ninh Thuan (Nui Chua NP) [38], Dong Nai (Vinh Cuu NR) [39], Kien Giang (Phu Quoc NP) [43] (This study; Csorba *et al.*, 2011; Kruskop, 2013).

Description

Medium-sized species with '*suilla*-type' dentition (Fig. 4, Tables 2 and 4). On the dorsal surface, the fur is warm brown. Ventrally, basal two-thirds of the hairs are uniformly white, the tips are brown or orange-brown, and the ventral surface is pure white. The plagiopatagium is attached to the base of the first toe claw.

Skull and dentition (Figs. 5 and 6). Rostrum is not inflated and the braincase is domed. Sagittal and lambdoid crests are well developed. I2 is partly anterior to I3. Upper C is higher than P4. C basal area is smaller than that of P4. P2 is much less in height than P4, and its basal area is half that of P4. M1 and M2 mesostyles are moderately developed. In the mandible, c exceeds p4 in height and basal area. The basal area of p2 varies from one-half to less than that of p4 and attains more than two-thirds its height. The talonids of m1 and m2 exceed their trigonids

in crown area, and their entoconids are equal to or slightly higher than their respective hypoconids.

Murina feae (Thomas, 1891)

Harpiocephalus feae Thomas, 1891: 884; Type locality: Biapo, Karin Hills, Burma.

Murina tubinaris: Corbet and Hill, 1992: 151 (part); Koopman, 1994: 132 (part); Simmons, 2005 (part); Francis *et al.*, 1999: 233 (part); Francis, 2008: 253 (part).

Murina cineracea Csorba and Furey, 2011: 896 (in Csorba *et al.*, 2011); Type locality: Cambodia, Mondulkiri Province, Seima Biodiversity Conservation Area.

Distribution

Myanmar, Thailand, Vietnam, Laos, and Cambodia (Thomas, 1891; Osgood, 1932; Francis *et al.*, 1999, Can *et al.*, 2008; Csorba *et al.*, 2011, Francis and Eger, 2012; Kruskop, 2013).

In Vietnam (Fig. 1): Lai Chau (Co Ma) [13], Son La (Phu Yen) [13], Phu Tho (Xuan Son NR) [12], Ha Giang (Duc Xuan area) [2], Tuyen Quang (Na Hang NR) [3], Bac Kan (Ba Be NP, Kim Hy NR) [4, 6], Thai Nguyen (Than Sa NR) [7], Vinh Phuc (Tam Dao NP) [1], Thanh Hoa (Pu Luong NR, Pu Hu NR, Xuan Lien NR) [16, 17, 19], Ninh Binh (Cuc Phuong NP) [18], Nghe An (Pu Hoat NR, Pu Mat NP, Pu Huong NR) [19, 21, 22], Ha Tinh (Vu Quang NP) [23], Quang Binh (Phong Nha-Ke Bang NP) [24], Quang Tri (Bac Huong Hoa NR, Dakrong NR) [25], Thua Thien-Hue (Bach Ma NP) [26], Quang Nam (Ngoc Linh NR) [28], Kon Tum (Ngoc Linh NR) [29], Gia Lai (Kon Ka Kinh NP) [32], and Dong Nai (Cat Tien NP) [40] (This study; Can *et al.*, 2008; Csorba *et al.*, 2011; Kruskop, 2013).

Description

Small to medium-sized species with '*suilla*-type' dentition (Fig. 4, Tables 2 and 4). The ear is evenly rounded and without an emargination. On the dorsal surface, the lower portion of individual hairs is dark brown, whereas the upper portion is light grey and terminates in a distinctly darker tip. Darkening of hair tips is more evident on the nape and the head, with an overall impression of dark greyish-brown and darker brown toward the head. The upper surface of the hind limbs, feet, and uropatagium are sparsely covered in short, uniformly dark brown hairs. On the ventral surface of the body, hairs are dark brown basally, whereas the upper portion is white. The ventral surface of the uropatagium is covered in relatively short uniformly white hairs, which are also present on the plagiopatagium adjacent to the body. The plagiopatagium is attached to the base of the toe claw.

Skull and dentition (Figs. 5 and 6). Rostrum is not inflated and the braincase is domed. There is no sagittal crest and the lambdoid crest is very weak. I2 is partly anterior to I3. C is slightly but evidently higher than P4, P2 is much less in height than P4. C basal area is smaller that of P4. M1 and M2 mesostyles are very weak. In the mandible, *c* slightly exceeds p4 in height and is equal or greater in basal area; p2 has less than one-half the basal area of p4 and attains more than two-thirds its height. The talonids of m1 and m2 equal their respective trigonids in crown area, and the entoconids of these teeth exceed their hypoconids in height. The postristid connects the hypoconid with the tip of the entoconid.

Karyotype

Karyotype (Fig. 7F and Table 5) based on a specimen from Thanh Hoa Province (Xuan Lien Nature Reserve) was 2n = 44, FN = 50. Autosomes consisted of three large metacentric pairs, one small submetacentric pair, and 17 medium-sized to small acrocentric pairs that gradually decrease in size. The X chromosome was identified as a medium-sized metacentric element.

Taxonomic note

Thomas (1891) described *Harpiocephalus feae* from Burma (Myanmar), but the species was considered a synonym of *M. aurata* since then (Tate 1941, Maeda, 1980; Corbet and Hill, 1992). Recently, Csorba *et al.* (2011) split *M. tubinaris* (Scully, 1881) into two species and restricted the distribution of *M. tubinaris* sensu stricto to Pakistan and northwest India. They described a new species, *M. cineracea,* that occurred from West Bengal and Arunachal Pradesh in India through Myanmar, Thailand, Laos to Vietnam. Francis and Eger (2012), however, based on the morphological study of the holotype, concluded that *M. feae* is actually a conspecific with *M. cineracea,* and therefore the name *M. feae* has priority over *M. cineracea*.

Murina eleryi Furey, Thong, Bates and Csorba, 2009

Murina aurata: Francis *et al*., 1999: 233 (part); Francis, 2008: 253 (part); Francis *et al*., 2010: 6 (part).

Murina eleryi Furey, Thong, Bates and Csorba, 2009: 226; Type locality: Kim Hy Commune, Na Ri district of Kim Hy Nature Reserve, Bac Kan province, Vietnam, 525 m a.s.l.; Francis and Eger, 2012: 28; Thomas *et al*., 2013: 231.

Distribution

Vietnam, Laos, and southern China in the provinces of Guizhou, Hunan, Guangdong, Guangxi

(Furey *et al.*, 2009; Francis and Eger, 2012; Liu *et al.*, 2014; Xu *et al.*, 2014).

In Vietnam (Fig. 1): Ha Giang [2], Cao Bang (Phia Oac-Phia Den NR) [5], Bac Kan (Kim Hy NR) [6], Phu Tho (Xuan Son NP) [12], Son La (Muong Do area) [13], Thanh Hoa (Xuan Lien NR) [19], Quang Binh (Phong Nha-Ke Bang NP) [24]; Quang Nam (Ngoc Linh NR) [28]; Kon Tum (Ngoc Linh NR) [29], Quang Ngai (Ba To area) [30] (This study; Furey *et al.*, 2009; Francis and Eger, 2012; Kruskop, 2013).

Description

Small species with '*suilla*-type' dentition (Fig. 4, Tables 2 and 4). Longer, shiny golden hairs with darker bases are scattered over the back, nape and head. On the dorsal surface, the lower portion of under hairs are very dark brown and are followed by a pale grey-yellow mid-section which progressively darkens to copper-reddish before terminating in a distinctly darker tip. The superficial impression is copper-reddish mottled with underlying dark brown and overlain by individual shiny gold hairs. Ventrally, the fur is black on the basal half and creamy white on the remainder, except the sides of the ventrum and upper chest, where hair tips graduate toward very light brown. The plagiopatagium is attached to the base of the first claw.

Skull and dentition (Figs. 5 and 6). Rostrum is not inflated and the braincase is moderately domed. No sagittal crest and the lambdoid crest is weak, but present. I2 is anterior to I3. C is higher than P4. C basal area is much smaller than that of P4. P2 basal area is less than half that of P4. M1 and M2 mesostyles are well developed. In the mandible, *c* distinctly exceeds p4 in height and is equal or slightly greater in basal area. The talonids of m1 and m2 are clearly separated from their trigonids and exceed these in crown area, and the entoconid clearly exceeds the hypoconid in height.

Taxonomic note

Francis *et al.* (1999), Furey and Tu (2006) and Francis (2008) reported specimens of *M. aurata* Milne-Edwards, 1872 from and around Vietnam. Furey *et al.* (2009), based on many specimens from northern Vietnam, described a new species, *M. eleryi*, and provided diagnostic characters to separate it from *M. aurata*. Thereafter, Francis and Eger (2012) suggested that all specimens from Laos and Vietnam formerly identified as *M. aurata*, to be referred to as *M. eleryi* or *M. harpioloides*. Therefore, we conclude that *M. aurata* does not occur in Vietnam and Laos. Xu *et al.* (2014) studied the genetic structure among specimens from southern China, Vietnam, and Laos, and suggested that a complicated phylogeographic pattern may exist.

Murina harpioloides Kruskop and Eger, 2008

Murina harpioloides Kruskop and Eger, 2008: 215; Type locality: Da Lat plateau, 30 km north-east from Da Lat, Lam Dong Province, Vietnam, about 1800 m a.s.l.

Distribution

Known only from Vietnam (Kruskop and Eger, 2008). In Vietnam (Fig. 1): Lam Dong (Bi Dup-Nui Ba NP and Da Lat plateau) [36] (This study; Kruskop and Eger, 2008; Abramov *et al.*, 2009).

Description

Small species with '*suilla*-type' dentition (Fig. 4, Tables 2 and 4). The fur of the dorsum is bicoloured in having dark brown under fur and a bright golden tip on the guard hairs. The dorsal guard hairs are dark brown at the base. The distal halves are tricoloured, with pale brown and darker brown rings and bright orange gold tips. Hair on the ventrum is dark brown at the base and tipped with pale silver grey. The entire tail membrane from the proximal to distal edge, and about one-third of the plagiopatagium next to the body, are covered dorsally with fur similar to guard hairs covering the body. Toes (up to the bases of claws), thumb, the upper side of the forearm and proximal part of the fifth metacarpal are covered with bright golden hairs.

Skull and dentition (Figs. 5 and 6). Rostrum is gradually sloped and the braincase is moderately rounded and domed. No sagittal crest and the lambdoid crest is very weak, but present. I2 is anterior to I3; C is similar in height as P4. C basal area is much smaller than that of P4. P2 much less in height than P4, and its basal area is less than half that of P4. M1 and M2 mesostyles are very weak. In the mandible, the lower canine possesses a small but distinct additional anterior cusp; c distinctly equals p4 in height and is equal or slightly greater in the basal area. The talonids of m1 and m2 are moderately separated from their trigonids, and the hypoconid distinctly exceeds the entoconid in height.

Taxonomic note

Kruskop and Eger (2008) described this species from Lam Dong province. Subsequently, Kruskop and Shchinov (2010) recorded *M.* cf. *harpioloides* from the Hoang Lien mountain range in northern Vietnam, far from the only previously known location of the species. Recently, Kruskop (2013)

re-identified this specimen as *M. chrysochaetes*, and indicated that *M. harpioloides* has more orange colouration of the guard hairs and a less domed braincase as compared to *M. chrysochaetes*. During the present study, two specimens were collected from the Bi Dup-Nui Ba National Park in the Lam Dong province, extending the known distribution of this species.

Murina chrysochaetes Eger and Lim, 2011

Murina chrysochaetes Eger and Lim, 2011: 228; Type locality: Diding Headwater Forest Nature Preserve, Jing Xi County, Guangxi Zhuang Autonomous Region, China, 978 m a.s.l.

Distribution

Known to occur in Vietnam and the Guangxi Zhuang Autonomous Region of southern China (Eger and Lim, 2011; Kruskop, 2013). In Vietnam (Fig. 1): Lao Cai (Hoang Lien NP) [1] (Kruskop, 2013), and Cao Bang (Phia Oac-Phia Den NR) [5] (This study).

Description

Small species with '*suilla*-type' dentition (Fig. 4, Tables 2 and 4). Ear is small, broad and round with little emargination on it is posterior edge. Tubular nostrils are proportionally long and the nostrils and the tip of the muzzle have a mid-brown pigmentation. The dorsum is a mix of black and gold bands, with gold mid-bands and dark tips, overlaid by long, gold-tipped guard hairs. The ventral pelage is dark at the base and the tips of the guard hairs are golden in colour.

Skull and dentition (Figs. 5 and 6). Rostrum is short and narrow. Braincase is highly domed, the slope of the forehead is abrupt. No sagittal crest and the lambdoid crest is very weak. I2 is anterior to I3; C equals P4 in height, and only half of it in basal dimensions; P2 is small, about half the height and one-third the crown area of P4. M1 and M2 mesostyles are reduced. The lower canine is the same height as p2, but exceeds it in basal area; p2 is small.

Taxonomic note

Eger and Lim (2011) described *M. chrysochaetes* from China, close to the border of northeast Vietnam. Kruskop (2013) recorded a single specimen from Hoang Lien Son Mountain in northern Vietnam. During the present study, a single specimen was collected from Phia Oac-Phia Den Nature Reserve, Cao Bang province. These known localities are restricted to high mountains around the borders of Vietnam and China.

Genus *Harpiocephalus* Gray, 1842

Diagnostic characters

A medium-sized vespertilionid bat with tubular nostrils. Total length of skull is over 20.0 mm. Dental formula: I2/3 C1/1 P2/2 M3/3 = 34. M3 is very reduced and peg-like. The incisors are shorter than the first upper premolar.

Harpiocephalus harpia (Temminck, 1840)

Vespertilio harpia Temminck, 1840: 219; Type locality: Mt. Gede, Java.

Harpiocephalus mordax Thomas, 1923:88; Type locality: Mogok, N Burma.

Harpiocephalus harpia: Hendrichsen *et al*., 2001: 105; Lunde *et al*., 2007: 160; Abramov *et al*., 2009: 67.

Distribution

Known to occur in India, Vietnam, Cambodia, Myanmar, Thailand, China, Malaysia, and Indonesia (Corbet and Hill, 1992; Koopman, 1994; Hendrichsen *et al.*, 2001; Matveev, 2005; Kruskop, 2013).

In Vietnam (Fig. 1): Lao Cai (Hoang Lien NP) [1], Tuyen Quang (Na Hang NR) [3], Bac Kan (Ba Be NP) [4], Cao Bang (Phia Oac-Phia Den NR) [5], Lang Son (Huu Lien NR) [8], Hai Phong (Cat Ba NP) [10], Nghe An (Pu Huong NR) [21], Quang Binh (Phong Nha–Ke Bang NP) [24], Kon Tum (Ngoc Linh NR) [29], Lam Dong (Bi Dup-Nui Ba NP) [36] (This study; Hendrichsen *et al.*, 2001; Lunde *et al.*, 2007; Thong and Furey, 2008; Abramov *et al.*, 2009; Kruskop and Shchinov, 2010).

Description

A medium-sized vespertilionid bat, but the largest species of the subfamily Murininae (Fig. 4, Tables 2, 3 and 4). The dorsal pelage has dark grey bases with a light reddish buff, and a rich, dark red tip. The ventral pelage is pale grey or reddish with dark bases. The wings are dark brown.

Skull and dentition (Figs. 5 and 6). Rostrum is short and broad and the braincase is domed. Sagittal and lambdoid crests are well developed. The dentition is robust. Upper canines are very strong. I2 height clearly exceeds that of I3. Both upper incisors are much lower in height than C. P2 smaller than P4 in basal dimensions, and are subequal in height. M1 and M2 have no mesostyle. M3 is reduced. In the mandible, the coronoid process is very prominent, c is well developed; p2 is less than p4 basally but equal in height.

Karyotype

The karyotype (Fig. 7G and Table 5) of the specimen from Kon Tum Province (Ngoc Linh Nature Reserve) was 2n = 44, FN = 52. Autosomes consisted of three large and one small metacentric pairs, one submetacentric pair, and 16 medium-sized to small acrocentric pairs, gradually decreasing in size. The X chromosome was a medium-sized metacentric, and the Y chromosome was a small acrocentric.

Taxonomic note

Harpiocephalus had been considered to include two species, *H. harpia* and *H. mordax* (Thomas, 1923; Hill and Francis, 1984; Corbet and Hill, 1992; Hendrichsen *et al.* 2001; Simmons, 2005), where *H. mordax* is greater and more robust in skull size and shape than *H. harpia*. Matveev (2005) reviewed the literature and specimens from Cambodia and indicated that male and female specimens differed in size and shape. These specimens purely fit with the view of Hill and Francis (1984) on *H. harpia* (male) and *H, mordax* (female), and molecular markers (Inter-SINE-PCR) clearly demonstrated specimens to be conspecifics (Matveev, 2004). Lin *et al.* (2006) reported the genus from Taiwan for the first time and considered *Harpiocephalus* a monotypic genus and *H. mordax* to be a synonym of *H. harpia* in reference to size differences between sexes. Sexual dimorphisms were also confirmed in the population in China (Zhou *et al.*, 2014; Chen *et al.*, 2015), and it is currently thought that only *H. harpia* exists.

There is no study on geographic variation of the widely distributed *H. harpia*. The karyotype of '*H. mordax*' from Thailand (McBee *et al.*, 1986) is 2n = 40. This is different from karyotypes reported in Taiwan and Guangdong Province, China (Lin *et al.*, 2006; Zhou *et al.*, 2014). Further morphological and molecular biological studies throughout the whole distribution area of *Harpiocephalus* should be performed.

Genus *Harpiola* Thomas, 1915

Diagnostic character

Small-sized vespertilionid bats with tubular nostrils: STOTL < 18.0. The dental formula is I2/3 C1/1 P2/2 M3/3=34. Both upper premolars (P2 and P4) and canine are similar in shape and size. I3 is large, robust and in contact with the upper canine. I3 is slightly larger than I2. The upper incisors exceed the half the height of the corresponding canines. P2 height is more than that of P4, and the lower canine is bicuspid.

Taxonomic note

Harpiola was described by Thomas (1915) based on *Murina grisea* Peters, 1872 as type species. Although, Ellerman and Morrison-Scott (1951), Corbet and Hill (1992), Koopman (1994) and Simmons (2005) treated *Harpiola* as a subgenus of *Murina*, Tate (1941), Bhattacharyya (2002), Kuo *et al.* (2006) and Kruskop *et al.* (2006) emphasized the considerable differences in skull and dentition between *Murina* and *Harpiola*, and accepted the valid generic status of *Harpiola*, which view is followed herewith.

Harpiola isodon Kuo, Fang, Csorba and Lee, 2006

Harpiola isodon Kuo, Fang, Csorba and Lee, 2006: 13; Type locality: Hualien County, Jhuosi Township, Yuli Wildlife Refuge, Taiwan, 23°32'N, 121°15'E, 2,000 m elevation; Kruskop, 2013: 176.

Harpiola cf. *isodon*; Kruskop *et al*., 2006: 14.

Distribution

Vietnam and Taiwan (Kuo *et al.*, 2006; Kruskop *et al.*, 2006; Kruskop and Shchinov, 2010; Kruskop, 2013). In Vietnam: (Fig. 1). Lao Cai (Hoang Lien NP) [1] and Kon Tum (Ngoc Linh NR) [29] (Kruskop *et al.*, 2006, Kruskop and Shchinov, 2010; Kruskop, 2013; this study).

Description

Medium-sized species of the subfamily (Fig. 4, Tables 2, 3 and 4). On the dorsal surface, hairs are very long and woolly; the basal part of underfur is dark brown with a bright yellow subterminal band and a dark brown tip. Guard hairs scattered all over the back are dark brown at the basal four-fifths with shiny golden yellow tips. From the ventral aspect, the fur is shorter, dark brown at the base and light brown in the terminal one-third. The dorsal side of the tail membrane, the tibia and the foot are all densely and evenly furred, including the last caudal vertebra, which is free from the uropatagium. The whole area of the tail membrane is also covered with dense, stiff, silvery grey hairs. The ear conch is possesses a very distinct emargination at the upper third of its posterior border. The tragus is moderately long (7.60 mm around), but wide at its base and gradually tapering to the backward-curved tip, which just reaches the level of the notch. The base of the tragus is with a small tooth-like projection at its outer margin.

Skull and dentition (Figs. 5 and 6). Rostrum is not inflated and the braincase is moderately domed. No sagittal crest and the lambdoid crest is weakly developed. Narial emargination is much longer than

wide. Basioccipital pits are well-defined, usually elongated and especially narrower posteriorly. I2 is a bit longer than the outer upper incisor (I3). Both upper incisors are about two-thirds that of C in height, and the basal area of the second upper incisor is more than two-thirds that of C. The basal area of C, P2, and P4 are subequal and they are gradually decreasing in height. The mesostyle of M1 and M2 is very weak, but recognizable. In the mandible, the lower canine has a well-developed additional cusp. The lower canines and premolar teeth are similar in bulk, and c is slightly less than p2 in height. Entoconid in m1 and m2 is lower than hypoconid, and formed a distinct cusp widely separated from metaconid.

Karyotype

Karyotype (Fig. 7H and Table 5) based on one specimen from Lao Cai province (Hoang Lien National Park) (IEBR-M5436) was 2n = 44, FN = 50. Autosomes consisted of three large metacentric pairs, one small submetacentric pair, and 17 medium-sized to small acrocentric pairs gradually decreasing in size. The X chromosome was a medium-sized metacentric.

Taxonomic note

This species was described as a second species of the genus *Harpiola* from Taiwan by Kuo *et al.* (2006). Kruskop *et al.* (2006) and Kruskop and Shchinov (2010) reported this species from Vietnam, and considered it to be conspecific with the population in Taiwan.

Discussion

Present and previous studies for karyotypes of the subfamily Murininae (Table 5; Harada, 1973; Ando *et al.*, 1977; McBee, 1986; Harada *et al.*, 1987; Ono and Obara, 1994; Lin *et al.*, 2002, 2006; Gu, 2006; Volleth, 2006; Wu *et al.*, 2010; Zhou *et al.*, 2011, 2014) emphatically indicated that all species karyotyped had 2n = 44, except for *Harpiocephalus harpia* (as *H. mordax*) reported by McBee (1986) from Thailand. Species of *Murina* and *Harpiola* share similar karyotypes, characterized by three large metacentric and one small submetacentric autosomal pairs, while *Harpiocephalus* differs in having an additional small submetacentric pair (no. 5). This feature is also shared with *H. harpia* populations in Taiwan and Guangdong, southern China (Lin *et al.*, 2006; Zhou *et al.*, 2014), and is suggested to have evolved by the inversion of the largest acrocentric pair in the *Murina* karyotype during the evolution of the genus *Harpiocephalus*. Except for *H. harpia*, conservative trends in chromosome rearrangements in the subfamily Murininae have been confirmed in this study, including additional species in the genus *Murina*. Cytological isolation mechanisms may not be responsible for the diversification of the genus *Murina*. Molecular data did not suggest clear relationships among lineages, but this may be interpreted as many lineages of the subfamily Murininae having been separated simultaneously and diverged thereafter. Future studies to examine the evolutionary history and mechanisms that enable such diversification within a short time period are needed.

Son *et al.* (2015) suggested that the important role of morphological diversification among the species of *Murina* in Vietnam is in the interaction among sympatric species pairs and between sexes. This is due to the observations from species that have diverged in the combination of size and shape of skulls, and sexual size dimorphism (i.e., larger females) with different dimorphic characteristics among species. Detailed analyses in this study of the sexual differences in *M. harrisoni* showed more complicated patterns of diversification. Sexual size dimorphism has not simply been achieved through differences in size and allometric-based shape, but through complicated size and shape differentiation due to the functional limitations and compensation of the skull. Continued observations of skulls (Fig. 9) may suggest that limiting factors for morphological variability exist in the nasal capsule or braincase, possibly in relation to echolocation function.

Distribution data and overall body size provide another interesting view for the interaction among sympatric species pairs. In each locality (Table 1), there were from one to seven species, except in the Kon Tum where 11 species were recorded, indicating a high species diversity among localities. This is probably because high mountains and primary forests enable the co-occurrence of multiple species through differences in altitudinal distribution (Fig. 10).

Among the 16 Murininae species in Vietnam, *Harpiocephalus harpia*, *M. cyclotis*, *M. annamitica*, *M. feae*, and *M. eleryi* were recorded from more than 10 localities (Table 1). Similar-sized species tend to separate by elevation as shown in Table 1 and Fig. 10. On the other hand, two medium-sized species, *M. cyclotis* and *M. feae,* are both found in lowland and overlap localities (Fig. 10 and Table 1).

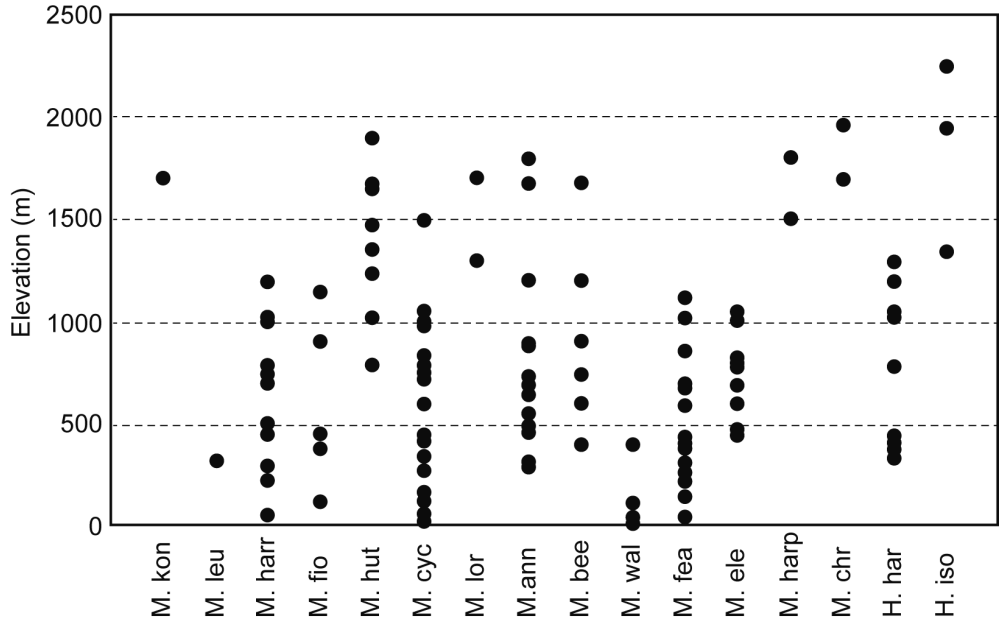

FIG. 10. Elevation distribution of specimens from species in the subfamily Murininae from Vietnam. Species names abbreviated to the first 3-4 letters

They provide an interesting example in that these two species clearly separate by STOTL in spite of overlapping FA (Fig. 11). We suggest that a morphological shift in skull size contributed to decreased interspecific competition among similar-sized species with overlapping FA. FA-STOTL plots (Fig. 11) also indicate that other species are well separated and only overlap in FA or STOTL among similar-sized species. In addition, the patterns of FA-STOTL shift for each species might not be parallel between males and females.

Forearm length and overall skull size have often been considered an indicator of overall size of bats, but we suggest that these two characteristics are related with completely different adaptations among species and between sexes. Wu *et al.* (2015) reported that echolocation call frequencies in *Rhinolophus* bats correlates with nasal capsule size in the skull, but did not relate to forearm length. In concordance with Son *et al.* (2015), we suggest that skull size and shape factors are affected by food habits and the echolocation function, whereas the FA and external morphology are more related to flight behaviour and aerial niche use.

Vietnam possesses the highest number of species of the subfamily Murininae in the world. Although

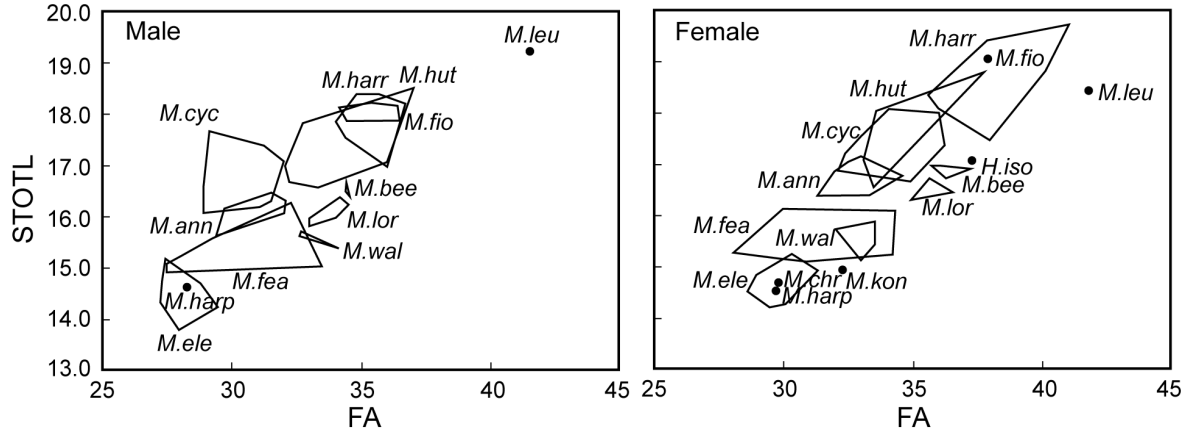

FIG. 11. Scatter plots between FA and STOTL of specimens from species in the genera *Murina* and *Harpiola* from Vietnam: male (A) and female (B)

this diversity may be a result of greater sampling effort within Vietnam, the complex geological history and biogeographic features of the country suggest a greater likelihood of complex speciation within this group of bats than perhaps exists in other countries of mainland southeast Asia. Our study also suggests that ecological adaptations, such as interactions among sympatric species pairs and intraspecific relationships between males and females, played important roles in the formation of taxonomic and morphological diversity. Understanding the reasons for the high species diversity as well as the evolutionary processes of the subfamily will require additional study on the taxonomy, distribution, ecology, and behavior of this group in Vietnam, and in Southeast Asia in general.

Acknowledgements

We are grateful to the Director, Nguyen Xuan Dang, Nguyen Quang Truong, Le Duc Anh, Tring Quang Phap (IEBR), Bui Tuan Hai (Vietnam National Museum of Nature), Hoang Trung Thanh, Le Duc Minh (Hanoi University of Science), and Nguyen Vu Khoi, Thomas O'Shea (Wildlife-at-Risk), Takafumi Nakano, Satoru Arai, Dai Fukui, Shin-ichiro Kawada for support with field survey, specimens, photo credit, and preparing distribution map. We are grateful to Sergei Kruskop (ZMMU), Judith Eger (ROM), Tamás Görföl, Péter Estók (HNHM) for kind support in loan of specimens and photos. We thank the Ministry of Agriculture, and staffs of Nature Reserves and National Parks in Vietnam for providing support to conduct field survey. This study was supported by the Japan Society for the Promotion of Science (JSPS) Ronpaku Program (VAST-11125), JSPS Core-to-Core Program B. Asia-Africa Scientific Platforms, VAST program for young researcher (IEBR.CBT. TS08.14/-05.2015), NSFC Major International Regional Joint Research Project Grant (31110103910), SYNTHESYS Project financed by the European Community Research Infrastructure Action under the FP7 'Capacities' Program, Hungarian Scientific Research Fund (OTKA) K112440, and JSPS Grants-in-Aid for Scientific Research (26304009).

Literature Cited

Abramov, A. V., V. V. Rozhnov, and P. N. Morozov. 2006. Notes on mammals of the Ngoc Linh Nature Reserve (Vietnam, Kon Tum province). Russian Journal of Theriology, 5: 85–92.

Abramov, A. V., S. V. Kruskop, and A. V. Sschinov. 2009. Small mammals of the Dalat Plateau, southern Vietnam. Russian Journal of Theriology, 8: 61–73.

Ando, K., T. Tagawa, and T. A. Uchida. 1977. Considerations of karyotypic evolution within Vespertilionidae. Experientia, 33: 877–879.

Anthony, E. L. P. 1988. Age determination in bats. Pp. 47–58, *in* Ecological and behavioral methods for the study of bats (T. H. Kunz, ed.). Smithsonian Institution Press, Washington, D.C., 479 pp.

Barlow, K. E., G. Jones, and E. M. Barratt. 1995. Can skull morphology be used to predict ecological relationships between bat species? A test using two cryptic species of pipistrelle. Proceedings of the Royal Society of London, 264B: 1695–1700.

Bates, P. J. J., and D. L. Harrison. 1997. Bats of the Indian subcontinent. Harrison Zoological Museum, Sevenoaks, UK, 258 pp.

Bates, P. J. J., Tin Nwe, M. J. Pearch, Khin Maung Swe, Si Si Hla Bu, and Thanda Tun. 2000. A review of bat research in Myanmar (Burma) and results of a recent survey. Acta Chiropterologica, 2: 53–82.

Bhattacharyya, T. P. 2002. Taxonomic status of the genus *Harpiola* Thomas, 1915 (Mammalia: Chiroptera: Vespertilionidae), with a report of the occurrence of *Harpiola grisea* (Peters, 1872) in Mizoram, India. Proceedings of the Zoological Society, Calcutta, 55: 73–76.

Blackith, R. E., and R. A. Reyment. 1971. Multivariate morphometrics. Academic Press, London, UK, ix + 412 pp.

Burmungsri, S., D. L. Harrison, C. Sarasook, A. Prajukjitr, S. Thong-Aree, and P. J. J. Bates. 2006. A review of bat research in Thailand with eight new species records for the country. Acta Chiropterologica, 8: 325–359.

Can, N. D., H. Endo, N. T. Son, T. Oshida, L. X. Canh, D. H. Phuong, D. P. Lunde, S. Kawada, A. Hayashida, and M. Sasaki. 2008. Checklist of wild mammal species of Vietnam. Primate Research Institute, Inuyama, Japan, 400 pp. [In English and Vietnamese].

Chen, B., W. Yu, Y. Wu, F. Li, Z. Xu, Q. Zhang, M. Harada, M. Motokawa, H. Peng, Y. Wang, and Y. Li. 2015. New record and sexual dimorphism of *Harpiocephalus harpia* in Guangxi and Jiangxi, China. Sichuan Journal of Zoology, 34: 211–215. [In Chinese with English abstract].

Corbet, G. B., and J. E. Hill. 1992. The mammals of the Indomalayan Region. Natural History Museum, London, 488 pp.

Csorba, G., and P. J. J. Bates. 2005. Description of a new species of *Murina* from Cambodia (Chiroptera: Vespertilionidae: Murininae). Acta Chiropterologica, 7: 1–7.

Csorba, G., V. D. Thong, P. J. J. Bates, and N. M. Furey. 2007. Description of a new species of *Murina* from Vietnam (Chiroptera: Vespertilionidae: Murininae). Occasional Papers, Museum of Texas Tech University, 268: 1–12.

Csorba, G., N. T. Son, I. Saveng, and N. Furey. 2011. Revealing cryptic bat diversity: three new *Murina* and redescription of *M. tubinaris* from Southeast Asia. Journal of Mammalogy, 92: 891–904.

Dobson, G. E. 1872. Notes on some bats collected by Captain W. G. Murray, in the North-Western Himalaya, with description of new species. Proceedings of the Asiatic Society of Bengal, 1872: 208–210.

Eger, J. L, and B. K. Lim. 2011. Three new species of *Murina* from Southern China (Chiroptera: Vespertilionidae). Acta Chiropterologica, 13: 227–243.

Eisenberg, J. F., and G. M. Mckay. 1970. An annotated checklist of the recent mammals of Ceylon with keys to the species. Ceylon Journal of Science (Biological Sciences), 8: 69–99.

Ellerman, J. R., and T. C. S. Morrison-Scott. 1951. Checklist of Palaearctic and Indian mammals 1758 to 1946. Trustees of the British Museum (Natural History), London, 810 pp.

Francis, C. M. 2008. A guide to the mammals of Southeast Asia. Princeton University Press, Princeton, 392 pp.

Francis, C. M, and J. Eger. 2012. A review of tube-nosed bats (*Murina*) from Laos with a description of two new species. Acta Chiropterologica, 14: 15–38.

Francis, C. M., A. Guillen, and M. F. Robinson. 1999. Order Chiroptera: Bats. Pp. 225–235, *in* Wildlife in Lao PDR: 1999 status report (J. W. Duckworth, R. E. Salter, and K. Khounboline, eds.). IUCN, Vientiane, Lao PDR, 275 pp.

Francis, C. M., A. V. Borissenko, N. V. Ivanova, J. L. Eger, B. K. Lim, A. G. Servent, S. V. Kruskop, I. Mackie, and P. D. N. Hebert. 2010. The role of DNA barcodes in understanding and conservation of mammal diversity in Southeast Asia. PLoS ONE, 5: e12575.

Furey, N. M., and V. T. Tu. 2006. The bat fauna of Khau Ca area, Vi Xuyen and Bac Me District, Ha Giang Province, northern Vietnam. Report to the Fauna and Flora International Vietnam Programme, 18 pp.

Furey, N. M., V. D. Thong, P. J. J. Bates, and G. Csorba. 2009. Description of a new species belonging to the *Murina* '*suilla*-group' (Chiroptera: Vespertilionidae: Murininae) from north Vietnam. Acta Chiropterologica, 11: 225–236.

Gray, J. E. 1842. Description of some new genera and fifty unrecorded species of Mammalia. Annals and Magazine of Natural History, 10: 255–267.

Gu, X. 2006. The Karyotypes of six species of bats from Guizhou. Chinese Journal of Zoology, 41(5): 112–116. [In Chinese with English abstract].

Hammer, Ø., D. A. Tharper, and P. D. Ryan. 2001. PAST: Paleontological statistics software package for education and data analysis. Palaeontologia Electronica 4: 9 pp. Available at http://palaeo-electronica.org/2001_1/past/ issue1_01.htm. Downloaded on 10 September 2012.

Harada, M. 1973. Chromosomes of nine Chiroptera species in Japan (Chiroptera). La Kromosoma, 91: 2885–2895.

Harada, M., K. Ando, T. A. Uchida, and T. H. Yosida. 1978. Karyological study of four Japanese *Myotis* bats (Chiroptera, Mammalia). Chromosoma, 5: 283–291.

Harada, M., K. Ando, T. A. Uchida, and S. Takada. 1987. A karyological study on two Japanese species of *Murina* (Mammalia: Chiroptera). Journal of the Mammalogical Society of Japan, 12: 15–23.

Hebert, P. D. N., A. Cywinska, S. L. Ball, and J. R. Dewaard. 2003. Biological identifications through DNA barcodes. Proceedings of the Royal Society, 270B: 313–321.

Hendrichsen, D. K., P. J. J. Bates, B. Hayes, and J. L. Walston. 2001. Recent records of bats (Mammalia: Chiroptera) from Vietnam with six species new to the country. Myotis, 39: 35–122.

Hill, J. E. 1964. Notes on some tube-nosed bats, genus *Murina*, from southeastern Asia, with descriptions of a new species and a new subspecies. Federation Museums Journal, 8: 48–59.

Hill, J. E., and C. M. Francis. 1984. New bats (Mammalia: Chiroptera) and new records of bats from Borneo and Malaya. Bulletin of British Museum of Natural History (Zoology), 46: 305–329.

Ith, S., G. Csorba, P. J. J. Bates, and N. M. Furey. 2011. Confirmation of seven bat species for Cambodia. Cambodian Journal of Natural History, 2011: 92–103.

Junggers, W. L., A. B. Falsetti, and C. E. Wall. 1995. Shape, relative size, and size-adjustments in morphometrics. Yearbook of Physical Anthropology, 38: 137–161.

Koopman, K. F. 1994. Chiroptera: systematics. Handbook of Zoology. Mammalia, Part 60. Walter de Gruyter, Berlin, 217 pp.

Kruskop, S. V. 2005. Towards the taxonomy of the Russian *Murina* (Vespertilionidae, Chiroptera). Russian Journal of Theriology, 4: 91–99.

Kruskop, S. V. 2013. Bats of Vietnam. Checklist and an identification manual. Joint Russian-Vietnamese Sciences and Technological Tropical Centre and Zoological Museum of Moscow M. V. Lomonosov State University, Moscow, 299 pp.

Kruskop, S. V., and J. L. Eger. 2008. A new species of tube-nosed bat *Murina* (Vespertilionidae, Chiroptera) from Vietnam. Acta Chiropterologica, 10: 213–220.

Kruskop, S. V., and A. V. Shchinov. 2010. New remarkable bat records in Hoang Lien Son mountain range, northern Vietnam. Russian Journal of Theriology, 9: 1–8.

Kruskop, S. V., M. V. Kalyakin, and A. V. Abramov. 2006. First record of *Harpiola* (Chiroptera, Vespertilionidae) from Vietnam. Russian Journal of Theriology, 5: 13–16.

Kuo, H.-C., Y.-P. Fang, G. Csorba, and L.-L. Lee. 2006. The definition of *Harpiola* (Vespertilionidae: Murininae) and the description of a new species from Taiwan. Acta Chiropterologica, 8: 11–19.

Kuo, H.-C., Y.-P. Fang, G. Csorba, and L.-L. Lee. 2009. Three new species of *Murina* (Chiroptera: Vespertilionidae) from Taiwan. Journal of Mammalogy, 90: 980–991.

Kuznetsov, G. V. 2006. Mammals of Vietnam. KMK Scientific Press Ltd., Moscow, 420 pp. [In Russian].

Lin, L.-K., M. Motokawa, and M. Harada. 2002. Karyology of ten vespertilionid bats (Chiroptera: Vespertilionidae) from Taiwan. Zoological Studies, 41: 347–354.

Lin, L.-K., M. Harada, M. Motokawa, and L.-L. Lee. 2006. Updating the occurrence of *Harpiocephalus harpia* (Chiroptera: Vespertilionidae) and its karyology in Taiwan. Mammalia, 70: 170–172.

Lindenfors, P., J. L. Gittleman, and K. E. Jones. 2007. Sexual size dimorphism in mammals. Pp. 16–26, *in* Sex, size, and gender roles: evolutionary studies of sexual size dimorphism (D. J. Fairbairn, W. U. Blanckenhorn, and T. Székely, eds.). Oxford University Press, Oxford, 278 pp.

Liu, Z., Y. Zhang, J. Zhang, and L. Zhang. 2014. *Murina eleryi* discovered in Hunan Province. Chinese Journal of Zoology, 49(1): 132–135. [In Chinese with English abstract].

Lunde, D. P., N. T. Son, and G. G. Musser. 2007. A survey of small mammals from Huu Lien Nature Reserve, Lang Son Province, Vietnam. Mammal Study, 32: 155–168.

Maeda, K. 1980. Review on the classification of little tube-nosed bats, *Murina aurata* group. Mammalia, 44: 531–551.

Maeda, K., and S. Matsumura. 1998. Two new species of vespertilionid bats, *Myotis* and *Murina* (Vespertilionidae: Chiroptera) from Yanbaru, Okinawa island, Okinawa Prefecture, Japan. Zoological Science, 15: 301–307.

Matveev, V. A. 2004. Systematics of the Old World Chiroptera derived from the insertions of DNA interspersed re-peats. PhD. Thesis, Moscow State University, Moscow, 293 pp. [In Russian].

Matveev, V. A. 2005. Checklist of Cambodian bats (Chiroptera), with new records and remarks on taxonomy. Russian Journal of Theriology, 4: 43–62.

Matveev, V. A., and G. Csorba. 2007. Bat fauna of Cambodia. Bat Research News, 48: 100–101.

McBee, K., J. W. Bickham, S. Yenbutra, J. Nabhitabhata,

and D. Schlitter. 1986. Standard karyology of nine species of vespertilionid bats (Chiroptera: Vespertilionidae) from Thailand. Annals of Carnegie Museum, 55: 95–116.

Milne-Edwards, A. 1868–74. Memoire sur la faune mammalogique du Tibet oriental et principalement de la principauté de Moupin. Pp. 231–379, *in* Recherches pour servir à l'histoire naturelle des mammifères: comprenant des considérations sur la classification de ces animaux (H. Milne-Edwards), 2 volumes. G. Masson, Paris.

Müller, J., K. Müller, C. Neinhuis, and D. Quandt. 2010. PhyDE – Phylogenetic data editor, version 0.9971. Released November 23, 2010, http://www.phyde.de.

Ono, T., and Y. Obara. 1994. Karyotypes and Ag-NOR variations in Japanese vespertilionid bats (Mammalia: Chiroptera). Zoological Science, 11: 473–484.

Osgood, W. H. 1932. Mammals of the Kelley-Roosevelts and Delacour Asiatic Expeditions. Publications of Field Museum of Natural History, Zoological Series, 18: 193–339.

Payner, R. W. 1987. Genstat 5 reference manual. Clarendon Press, Oxford, 749 pp.

Peters, W. 1872. Mittheilung über neue Flederthiere. Monatsbericht der Königlich Preussischen Akademie der Wissenschaften zu Berlin, 1872: 256–264.

Posada, D. 2008. jModelTest: Phylogenetic model averaging. Molecular Biology and Evolution, 25: 1253–1256.

Reyment, R. A. 1971. Multivariate normality in morphometric analysis. Mathematical Geology, 3: 357–368.

Ronquist, F., M. Teslenko, P. Van Deer Mark, D. L. Ayres, A. Darling, S. Hohna, B. Larget, L. Liu, M. A. Suchard, and J. P. Huesenbeck. 2012. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. Systematic Biology, 61: 539–542.

Ruedi, M., J. Biswas, and G. Csorba. 2012. Bat from the wet: two new species of tube-nosed bats (Chiroptera: Vespertilionidae) from Meghalaya, India. Revue Suisse de Zoologie, 119: 111–135.

Scully, J. 1881. On the mammals of Gilgit. Proceedings of the Zoological Society of London, 1881: 197–209.

Simmons, N. B. 2005. Order Chiroptera. Pp. 312–529, *in* Mammal species of the World: a taxonomic and geographic reference, 3rd edition (D. E Wilson and D. M. Reeder, eds.). Johns Hopkins University Press, Baltimore, MD, 2142 pp.

Smith, A. T. and Y. Xie. 2008. A guide to the mammals of China. Princeton University Press, Princeton, 544 pp.

Soisook, P. 2011. A checklist of bats (Mammalia: Chiroptera) in Thailand. Journal of Wildlife in Thailand, 18: 121–151.

Soisook, P., S. Karapan, C. Satasook, and P. J. J. Bates. 2013*a*. A new species of *Murina* (Mammalia: Chiroptera: Vespertilionidae) from peninsular Thailand. Zootaxa, 3746: 567–579.

Soisook, P., S. Karapan, C. Satasook, V. D. Thong, F. A. A. Khan, I. Maryanto, G. Csorba, N. Furey, B. Aul, and P. J. J. Bates. 2013*b*. A review of the *Murina cyclotis* complex (Chiroptera: Vespertilionidae) with descriptions of a new species and subspecies. Acta Chiropterologica, 15: 271–292.

Son, T. N., M. Motokawa, T. Oshida, V. D. Thong, G. Csorba, and H. Endo. 2015. Multivariate analysis of the skull size and shape in tube-nosed bats of the genus *Murina* (Chiroptera: Vespertilionidae) from Vietnam. Mammal Study, 40: 79–94.

Swofford, D. L. 2003. PAUP*: phylogenetic analysis using parsimony (*and other methods), version 4. Sinauer Associates, Sunderland, Massachusetts.

Tate, G. H. H. 1941. Results of the Archbold expeditions no. 40: notes on vespertilionid bats of the subfamilies Miniopterinae, Murininae, Kerivoulinae and Nyctophilinae. Bulletin of the American Museum of Natural History, 78: 567–597.

Temminck, C. J. 1835–1841. Monographies de mammalogie ou description de quelques genres de mammifères, dont les espèces dont été observées dans les différens musées de l'Europe. Volume 2. C.C. van der Hoek, Leiden, 392 pp.

Thomas, N. M., J. W. Duckworth, B. Douangboubpha, M. Williams, and C. M. Francis. 2013. A checklist of bats (Mammalia: Chiroptera) from Lao PDR. Acta Chiropterologica, 15: 193–260.

Thomas, O. 1891. Diagnoses of three new mammals collected by Signor L. Fea in the Carin Hills, Burma. Annali del Museo Civico di Storia Naturale di Genova, 30 (2, 10): 884.

Thomas, O. 1914. New Asiatic and Australian bats and a new bandicoot. Annals Magazine Natural History, 13: 439–444.

Thomas, O. 1915. A special genus for the Himalayan bat known as *Murina grisea*. Annals and Magazine of Natural History, 8, 16: 309–310.

Thomas, O. 1923. Scientific results from the mammal survey. XLI. On the forms contained in the genus *Harpiocephalus*. Journal of the Bombay Natural History Society, 29: 8889.

Thong, V. D. and N. M. Furey. 2008. The bat fauna of Cat Ba Biosphere Reserve. Journal of Biology, 30: 73–77 [In Vietnamese with English summary].

Thong, D. V., D. C. Dietz, A. Denzinger, P. J. J. Bates, N. M. Furey, G. Csorba, G. Hoye, L. D. Thuy, and H.-U. Schnitzler. 2011. Further records of *Murina tiensa* from Vietnam with first information on its echolocation calls. Hystrix, the Italian Journal of Mammalogy, 22: 129–138.

Tordoff, A. W., T. M. Hieu, T. Q. Ngoc, E. Sterling, P. Sweet, T. Chesser, B. K. Kevin, J. Eger, B. Lim, D. Harder, *et al.* 2000. A feasibility study for the establishment of Ngoc Linh Nature Reserve, Quang Nam Province, Vietnam. Birdlife International Vietnam Programme, Hanoi, Vietnam, 74 pp.

Trai, L. T., W. J. Richardson, B. D. Tuyen, L. V. Cham, N. H. Dung, H. V. Hoach, A. L. Monastyrskii, and J. C. Eames. 1999. An investment plan for Ngoc Linh Nature Reserve, Kon Tum Province, Vietnam: a contribution to the management plan. BirdLife International Vietnam Programme, Hanoi, Vietnam, 106 pp.

Trai, T. L., L. V. Cham, T. Q. Ngoc, T. M. Hieu, N. V. Sang, A. L. Monastyrskii, B. D. Hayes, and J. C Eames. 2000. An investment plan for Kon Ka Kinh Reserve, Gia Lai province, Vietnam: A contribution to the management plan. BirdLife International Vietnam Programme, Hanoi, 77 pp.

Tu, T. V., R. Cornette, J. Utge, and A. Hassanin. 2015. First records of *Murina lorelieae* (Chiroptera: Vespertilionidae) from Vietnam. Mammalia, 79: 201–213.

Volleth, M. 2006. Karyotype analysis of *Murina suilla* and *Phoniscus atrox* from Malaysia (Chiroptera: Murininae, Kerivoulinae). Lynx (Praha), 37: 275–284.

Wu, H., T.-L. Jiang, R. Müller, and J. Feng. 2015. The allometry of echolocation call frequencies in horseshoe bats: nasal capsule and pinna size are the better predictors than forearm length. Journal of Zoology (London), 297: 211–219.

Wu, Y., M. Motokawa, Y. Li, M. Harada, Z. Chen, and W. Yu. 2010. Karyotype of Harrison's tube-nosed bat *Murina harrisoni* (Chiroptera: Vespertilionidae: Murininae) based on the second specimen recorded from Hainan Island, China. Mammal Study, 35: 277–279.

Xu, Z., W. Yu, Y. Wu, F. Li, B. Chen, M. Harada, M. Motokawa, Y. Gong, and Y. Li. 2014. Preliminary study on population genetic structure and taxonomy of Elery's tube-nosed bat (*Murina eleryi*). Acta Theriologica Sinica, 34: 270–277. [In Chinese with English abstract].

Zhou, Q., Y. Zhang, M. Motokawa, M. Harada, Y. Gong, Y. Li, and Y. Wu. 2011. A new record bat *Murina huttoni* from Guangdong, China and its morphology, karyotypes, echolocation calls. Chinese Journal of Zoology, 46(1): 109–114. [In Chinese with English abstract].

Zhou, Q., Z. Xu, W. Yu, F. Li, B. Chen, Y. Gong, M. Harada, M. Motokawa, Y. Li, and Y. Wu. 2014. The occurrence of bat *Harpiocephalus harpia* from Nanlin, Guangdong and its karyotypes, echolocation calls. Chinese Journal of Zoology, 49(1): 41–45. [In Chinese with English abstract].

Received 29 July 2015, accepted 05 November 2015

Appendix I

Localities for the specimens of the subfamily Murininae from Vietnam used in this study. Locality numbers correspond with Fig. 1

1. Lao Cai (Hoang Lien NP); 2. Ha Giang (Duc Xuan area; Vi Xuyen area; Khau Ca NR); 3. Tuyen Quang (Na Hang NR); 4. Bac Kan (Ba Be NP); 5. Cao Bang (Phia Oac-Phia Den NR); 6. Bac Kan (Kim Hy NR); 7. Thai Nguyen (Than Sa NR); 8. Lang Son (Huu Lien NP); 9. Quang Ninh (Bai Tu Long NP); 10. Hai Phong (Cat Ba NP); 11. Vinh Phuc (Tam Dao NP; Me Linh and Tam Dao NP); 12. Phu Tho (Xuan Son NP); 13. Son La (Co Ma area; Ta Sua NR); 14. Son La (Thuan Chau); 15. Son La (Xuan Nha NR); 16. Thanh Hoa (Pu Hu NR); 17. Thanh Hoa (Pu Luong NR); 18. Ninh Binh (Cucc Phuong NP); 19. Thanh Hoa (Xuan Lien NR); 20. Thanh Hoa (Ben En NP); 21. Nghe An (Pu Huong NR); 22. Nghe An (Pu Mat NP); 23. Ha Tinh (Vu Quang NP); 24. Quang Binh (Phong Nha-Ke Bang NP); 25. Quang Tri (Bac Huong Hoa NR; Dak Rong NR); 26. Thua Thien-Hue (Bach Ma NP); 27. Quang Nam (Song Thanh NR); 28. Quang Nam (Ngoc Linh NR); 29. Kon Tum (Ngoc Linh NR); 30. Quang Ngai (Ba To area); 31. Kon Tum (Chu Mom Ray NP); 32. Gia Lai (Kon Ka Kinh NP); 33. Binh Dinh and Phu Yen (Hoa Son area); 34. Dak Lak (Yok Don NP); 35. Dak Lak (Chu Yang Sin NP); 36. Lam Dong (Bi Dup-Nui Ba NP); 37. Khanh Hoa (Hon Ba NR); 38. Ninh Thuan (Nui Chua NP); 39. Dong Nai (Cat Tien NP); 40. Dong Nai (Vinh Cuu NR); 41. Binh Phuoc (Bu Gia Map NP); 42. Ba Ria-Vung Tau (Con Dao NP); 43. Kien Giang (Phu Quoc NP).

Appendix II

Specimens of the subfamily Murininae used in this study. Asterisk (*) indicates specimens examined for karyotype

M. kontumensis sp. nov. (*n* = 1) — Kon Tum [29]: IEBR-M5697* (holotype) (F)

M. leucogaster (*n* = 2) — Nghe An (Pu Mat NP) [22]: HZM1.31758 (F). China: Sichuan: IBHG10122 (M).

M. harrisoni (*n* = 21) — Son La [15]: HNHM 2010.42.1 (M); Phu Tho [12]: Thong Coll.T2, IEBR T.290708.7 (M); Bac Kan [6]: HZM.2.38178 (holotype of *tiensa*) (F), HNHM 2007.28.1 (paratype of *tiensa*), HZM NF 301006.1 (M); Vinh Phuc [11]: HNHM 2009.6.2 (F), IEBR-M4998 (M); Hai Phong [10]: IEBR T.220408.2 (F); Thanh Hoa [19]: IEBR-M6033 (F), Nghe An [22]: IEBR-M3299; HZM 1.31525 (F); Dak Lak [34]: ROM 107750 (F), 107739, 107749 (M); Cambodia: HZM 1.36316 (holotype), CBC 01290 (F); China: Hainan: IBGH 8295 (F); China: Guangxi: ROM 116463 (F), ROM 116468 (M); Thailand: SMF 53218 (M).

M. fionae (*n* = 7) — Quang Nam [27]: IEBR-M3080 (M); Kon Tum [31]: IEBR-M5075 (M); Gia Lai [32]: IEBR-M3588 (M); Quang Ngai [30]: IEBR-M3635 (F), M3902, M3917 (M); Dong Nai [40]: HNHM 22858 (M).

M. huttoni (*n* = 27) — Lao Cai [1]: ZMMU S186525, IEBR-M5434, M5435*, M5437* (F), ZMMU S186700, IEBR-M5428*, M5480*, M5482 (M); Cao Bang [5]: IEBR-M6023; Quang Tri [25]: IEBR-M3153 (F); Kon Tum [29]: IEBR-M5644, M5693* (F), VN11 1543, M5640*, M5641, M5643, M5653, M5696 (M); Dak Lak [35]: HNHM 22885 (F); Lam Dong [36]: IEBR-M5407*, M5413, M5415*, M5416 (F), M4718, M5419 (M); Khanh Hoa [37]: ZMMU S175150, ZMMU S175151 (M).

M. cyclotis (*n* = 75) — Son La [14, 15]: IEBR-M3046, M4678 (M); Phu Tho [12] IEBR-M4052*, M4071* (M); Ha Giang [2]: IEBR-M4753* (M); Cao Bang [5]: IEBR M5631, M5630, M6001 (F); IEBR M5627, M5628, M5629, M6000 (M); Bac Kan [4] IEBR-M1210, M4561 (F), M4562 (M); Tuyen Quang [3]: IEBR-M0492, M5394 (F), M0505, M1887, M1891, M4976, M5296, M5309, IEBR VN11-1562 (M); Vinh Phuc [11]: IEBR-M4560 (F); Quang Ninh [9]: IEBR-M2855, M3128, M3131 (F), M3129, M3132, M3133, M3134 (M); Ninh Binh [18]: HNHM22919/2008.23.1 (F); Thanh Hoa [16, 17, 19] IEBR-M3725, M3726, M4223*, M6034, M6039, M6040 (F), M3736, M3738, M4126, M6036, M6038, M4172 (M); Nghe An [21, 22]: HNHM 22925, IEBR-M1359, M1632, M3316, M3330 (F), M1390, M2180, M4119, M4120, M3054, M3069, M3320 (M); Quang Binh [24]: IEBR-M3868, M3872, M3876 (F), M3874, M3875, M5333 (M); Quang Tri [25]: IEBR-M4953 (F), M4942* (M); Kon Tum [29]: IEBR-M5338 (M); Gia Lai [32]: IEBR-M3607 (M); Lam Dong [36]: IEBR-M5776 (M); Quang

Appendix II. Continued

Ngai [30]: IEBR-M3645, M3646, M3651 (F), M3632 (M); Phu Yen [33]: IEBR-M4187 (M); Dong Nai [40]: IEBR-M4591 (M); Binh Phuoc [41]: ZMMU S184674 (F).

M. lorelieae (*n* = 10) — Kon Tum [29]: VN11-1161, 1223, IEBR-M5656 (F); VN11-1220, IEBR-M5648*, M5651, M5662, M5663, HNHM B20140915.5, 20140915.7* (M)

M. annamitica (*n* = 22) — Son La [15]: IEBR-M3034 (F), M2997 (M); Lao Cai [1] IEBR-M5429 (F), ZMMU S184673 (M); Tuyen Quang [3] IEBR-M4508 (M); Thanh Hoa [17] IEBR-M4122, M4124 (M); Nghe An [21, 22] IEBR-M2181 (F), HNHM 22929, IEBR-M1600, M3327 (M); Quang Tri [25] IEBR-M3148, M3167 (F); Kon Tum [29] IEBR-M4131 (F); Quang Ngai [30] IEBR-M3630, M3639, M3640, M3643, M4718 (F), M3633, M3650, M3652 (M).

M. beelzebub (*n* = 10) — Quang Tri [25]: IEBR-M3636, M4842*, M5645, M5760 (paratype), VN11-1586, HNHM 2007.50.7 (paratype) (F), HNHM 2007.50.24 (holotype) (M); Kon Tum [29]: IEBR Tu071211.1, M5645 (F), IEBR-M4149, M5646 (M); Quang Ngai [30] IEBR-M3636 (F), M3904 (M).

M. walstoni (*n* = 9) — Yok Don [34]: IEBR-M1480, HNHM 22933 (F), IEBR-M1481 (M); Ninh Thuan [38]: IEBR-M6030, M6031, M6032 (F); Dong Nai [40]: IEBR-M4592 [F); Kien Giang: IEBR-M2479, M2920 (M).

M. feae (*n* = 38) — Son La [14]: HNHM 2010.42.2, IEBR-M4679 (F); Ha Giang [2] IEBR-M3264 (M); Tuyen Quang [3]: IEBR-M0495 (F), IEBR-M504, M5350, (M); Bac Kan [4]: IEBR-M4563 (F); IEBR-M323, M4510, HNHM 2000.84.7 (M); Vinh Phuc [11]: IEBR-M4991, M5056 (M); Ninh Binh [18]: IEBR-M5054 (F); Thanh Hoa [16, 17, 19]: HNHM 2000.84.4, IEBR-M3718, M3728, M4123, M4127, M4214*, VN110495 (F), HNHM 2000.84.7, IEBR-M3722, M4121, M4125 (M); Nghe An [21, 22]: IEBR-M1360, M1387.1/22868 (F), IEBR-M1363, M1364, M3068 (M); Ha Tinh [23]: IEBR-VN110001, 0007; Quang Binh [24]: IEBR-M3867, M3870, M3871 (F), M3869, M3873 (M); Quang Tri [25] IEBR-M3154, M4116 (M); Kon Tum [29]: IEBR-M5719 (M); Dong Nai [39]: IEBR-M323/22860 (M).

M. eleryi (*n* = 19) — Son La [14]: IEBR-T.241107.1 (M); Phu Tho [12] IEBR-M4070 (M); Ha Giang [2]: NF.250506.1 (M); Cao Bang [5]: IEBR-M5622 (F); M6024 (M); Bac Kan [6]: BMNH 2008.25, ROM-NF.240507.1, HZM.1.39006, NF.230707.1, 240707.2, HNHM 2007.28.2 (paratype) (F), HNHM 2007.51.1 (holotype), NF.170906.3, 030707.1 (M); Thanh Hoa [19]: IEBR-M6035 (M); Quang Binh [30]: IEBR-M3866 (F); Kon Tum [29]: IEBR-M5718 (F); Quang Ngai [35]: IEBR-M4511 (F), IEBR-M3644 (M).

M. harpioloides (*n* = 3) — Lam Dong [44]: ZMMU S173401 (F), IEBR-M5806 (F), IEBR-M5860 (M).

M. chrysochaetes (*n* = 2) — Cao Bang [5]: IEBR-M6020 (F), Lao Cai [13]: ZMMU S186699 (F).

Harpiocephalus harpia (*n* = 5) — Cao Bang [5]: IEBR-M6037 (M); Tuyen Quang [3]: IEBR-M422 (F); Nghe An [21]: IEBR-M1362, M1391 (F); Kon Tum (Ngoc Linh NR): IEBR-M5661* (M).

Harpiola isodon (*n* = 1) — Lao Cai [1]: IEBR-M5436* (F).

Appendix III

GenBank/BOLD accession numbers for published COI sequences used in this study

Murina harrisoni: Vietnam: HM540980, 540981, 540982; Laos: HM540983; China: HM540984. *M. leucogaster*: China: HM540987. *M. fionae*: Vietnam: HM540966; Laos: HM540965. *M. huttoni*: Vietnam: JQ601542, KF772782; Laos: HM540976; China: HM540978, 540979, JQ601452, 601454, 601455. *M.* cf. *cyclotis*: Vietnam: JQ601536, HM540953, JQ601535, JQ601538, 601544, KF772775, 772776; Laos: HM540940, 540941, 540944, 540945, 540946, 540947, 540952; China: HM540948, 540949, 540950, 540951; India: HM540939. *M. lorelieae*: Vietnam: KF772780; China: JN082179. *M. annamitica*: Laos: HM540967, 540968, 540971, JQ601528, 601530, 601531, 601532, 601533, 601534. *M. walstoni*: Laos: HM540958. *M. feae* and *M. beelzebub* (examined by Francis *et al.* [2012] as *M. feae*): Vietnam: HM541000, JQ601539, 601540, 601541, KF772777; Laos: HM540993, 540994, 540995, 540997, 540999; China: JQ601463, 601519, 601526. *M. eleryi*: Vietnam: HM540933; Laos: HM540931; China: HM540935, 540937. *M. harpioloides*: Vietnam: HM540975. *M. chrysochaetes*: China: HM540986, JQ601461, 601464, 601468, 601469, 601478, 601496, 601518, 601524, 601525. *M. aenea*: Malaysia: ADQ50994, HM540929. *M. balaensis*: Thailand: PSUZC MM2012-214. *M. gracilis*: Taiwan: KJ198513, 198514, 198527, 198538, 198540, 198542, 198556, 198565, 198570. *M. guilleni*: Thailand: HM540955. *M. hilgendorfi*: China: JF442833; Russia: JF442834, 442835, 442836, 442839, 442840, 442841. *M. peninsularis*: Malaysia: HM540972, 540973. *M. recondita*: Taiwan: KJ198578, 198583, 198592, 198603, 198619. *M. shuipuensis*: China: JN082180. *M. suilla*: Malaysia: HM540989, 540990, 540991. *M ussuriensis*: Russia: JF442842, 442843, 442844, 442848, 442850. *Harpiocephalus harpia*: Laos: HM540283. *Harpiola isodon:* Vietnam: HM540286. *Myotis muricola*: Vietnam: HM914942. *Kerivoula* cf. *hardwickii*: Vietnam: HM540687.