

First record of Disk-footed bat *Eudiscopus denticulus* (Osgood, 1932) (Chiroptera: Vespertilionidae) from India with notes on its ecology and genetics

Authors: Saikia, Uttam, Chakravarty, Rohit, Hegde, Vishwanath D., Meetei, Asem Bipin, Kruskop, Sergei, et al.

Source: *Revue suisse de Zoologie*, 128(1) : 187-198

Published By: Muséum d'histoire naturelle, Genève

URL: <https://doi.org/10.35929/RSZ.0044>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

**First record of Disk-footed bat *Eudiscopus denticulus* (Osgood, 1932)
(Chiroptera: Vespertilionidae) from India with notes on its ecology and genetics**

Uttam Saikia¹, Rohit Chakravarty², Vishwanath D. Hegde¹, Asem Bipin Meetei¹, Sergei Kruskop³,
Gabor Csorba⁴ & Manuel Ruedi^{5*}

¹ Zoological Survey of India, North Eastern Regional Centre, Risa Colony, Shillong, Meghalaya-793003, India

² Department of Evolutionary Ecology, Leibniz Institute for Zoo and Wildlife Research, Alfred-Kowalke-Str. 17, D-10315 Berlin, Germany

³ Zoological Museum of Moscow State University, Ul. Bolshaya Nikitskaya 2, 125009 Moscow, Russia

⁴ Department of Zoology, Hungarian Natural History Museum, Baross 13., H-1088 Budapest, Hungary

⁵ Department of Mammalogy and Ornithology, Muséum d'histoire naturelle, C.P. 6434, CH-1211 Genève 6, Switzerland

* Corresponding author: manuel.ruedi@ville-ge.ch

Abstract: On the basis of two recently collected specimens from Meghalaya state in north-eastern India, we report the occurrence of the monotypic vespertilionid genus *Eudiscopus* in the Indian Subcontinent. This taxon has so far been known only from a few localities in Southeast Asia. Our records also constitute a westward range extension of *E. denticulus* by about 1000 km into eastern South Asia. We provide comparative mensural data of several museum specimens of *E. denticulus* from Southeast Asia. Additionally, the echolocation call and wing characteristics of this species from Meghalaya are also described. The higher call frequency and lower wing loading and aspect ratio of the Indian *E. denticulus* indicate adaptation to cluttered environment, corroborating its guild assignment as edge space aerial forager. Molecular comparisons of the mitochondrial cytochrome *b* gene sequence with samples from Vietnam revealed no genetic variation, despite large geographic distances separating the samples. Phylogenetic reconstructions confirm that *Eudiscopus* is a basal Myotinae, but its position relative to *Submyotodon* and *Myotis* is still uncertain.

Keywords: Phylogeny - Myotinae - echolocation - wing morphology - India.

Résumé: En se basant sur deux spécimens découverts dans l'état du Meghalaya, au nord-est de l'Inde, nous révélons l'existence d'*Eudiscopus denticulus* pour la première fois dans le sous-continent indien. Ce genre monotypique n'était connu que de quelques localités en Asie du Sud-Est. Cette découverte au Meghalaya étend par conséquent l'aire connue pour cette espèce de près de 1000 km vers l'ouest. Des données biométriques comparatives avec des spécimens d'Asie du Sud-Est sont présentées. De même, les cris d'écholocation et la morphologie alaire d'*E. denticulus* du Meghalaya sont aussi analysés. Une combinaison de signaux ultrasonores particulièrement brefs et aigus, ainsi qu'une faible charge alaire couplée à des ailes relativement larges suggèrent qu'*E. denticulus* est adapté à chasser dans des milieux encombrés, ce qui corrobore son classement dans cette guild de chauves-souris insectivores. Des séquences mitochondriales du gène cytochrome *b* sont aussi comparées avec des échantillons vietnamiens et malgré la grande distance géographique qui les sépare, elles ne révèlent aucune différence génétique. Les reconstructions moléculaires basées sur ce marqueur démontrent que le genre *Eudiscopus* fait bien partie d'une lignée basale parmi les Myotinae, mais sa position exacte relativement aux genres *Submyotodon* et *Myotis* reste ambiguë.

Mots-clés: Phylogénie - Myotinae - écholocation - morphologie alaire - Inde.

INTRODUCTION

The Disk-footed bat, *Eudiscopus denticulus* (Osgood, 1932), is an Oriental species known from a few localities in Myanmar, Thailand, Laos, and Vietnam (Soisook *et al.*, 2016), and in Yunnan, China (Yu *et al.*, 2021). It was originally described as *Discopus denticulus* based on several specimens captured from Phong Saly (Phongsali) in northernmost Laos (Osgood, 1932) but later allocated to the genus *Eudiscopus* as the former was found to be preoccupied (Conisbee, 1953). This enigmatic species of Vespertilionidae has been allocated variously to the subfamily Vespertilioninae (Tate, 1942; Simmons, 2005; Görfföl *et al.*, 2019), or, more commonly, as a member of the Myotinae, with uncertain position (Borissenko & Kruskop, 2003; Tsytsulina *et al.*, 2007; Borisenko *et al.*, 2008; Yu *et al.*, 2014; Amador *et al.*, 2018;). In view of its relatively wide distribution, the IUCN categorized it as Least Concern although nowhere it is a common species and it is rarely found in museum collections (Tsytsulina *et al.*, 2007; Soisook *et al.*, 2016; Haslauer, 2019; Yu *et al.*, 2021). In this paper, based on two new specimens collected from Meghalaya state in north-eastern India, we provide the first evidence of this species in the Indian Subcontinent together with comparative data of this species from Southeast Asia. Echolocation call characteristics of a free flying animal and its wing morphology in relation to ecology are also discussed. Finally, we compare a fragment of the mitochondrial cytochrome *b* gene sequenced from a Meghalaya specimen with samples from Vietnam and place this lineage of *Eudiscopus* in a more general phylogenetic context.

MATERIALS AND METHODS

Two individuals of *Eudiscopus denticulus* from Meghalaya were captured with mist nets set in a forest patch of overgrown bamboo adjacent to the Nongkhylliem Wildlife Sanctuary, in Ri-Bhoi district of Meghalaya, India (25°56'13"N, 91°46'24"E, 210 m a.s.l.), on July 1st 2020. Animals were handled following standard methods in mammalogy (Sikes *et al.*, 2016) and kept as vouchers in the collection of the Zoological Survey of India, Shillong (ZSI) for further morphologic and genetic examinations. For morphological comparisons with extra-Indian material, collections of the following institutions were consulted: AMNH, The American Museum of Natural History, New York, USA; BM(NH), The Natural History Museum [formerly British Museum (Natural History)], London, UK; HNHM, Hungarian Natural History Museum, Budapest, Hungary; IEBR, Institute of Ecology and Biological Resources, Hanoi, Vietnam; MHNG, Natural History Museum of Geneva, Switzerland; ZMMU, Zoological Museum of Moscow State University, Moscow. The examined *E. denticulus* specimens included the type from Laos [BM(NH)

40.819] and 18 other individuals from Southeast Asia as follows: Myanmar, Pegu – AMNH 54789 and 54790 (2 females); Vietnam, Pu Huong – IEBR PH8, 10, 14-18, 20, 23, 31 and 33 (unsexed), and HNHM 2008.23.12., 2012.30.29., 2012.30.30., 2012.30.31., 2012.30.32 (3 females and 2 males).

Animals were characterized biometrically with 11 external and 14 craniodental morphological characters. Except for hindfoot length (HF) which included claws, the standard external measurements were taken as defined by Bates & Harrison (1997) and taken to the nearest 0.1 mm with a dial calliper. These external measurements were forearm length (FA), tail length (TL), head and body length (HB), tibia length (TB), ear length (E), tragus length (TR), length of the three respective metacarpals (3mt to 5mt) and body mass (W, expressed in grams). For vouchered specimens, craniodental measurements were also taken with a digital calliper (to the nearest 0.01 mm) and also corresponded to those proposed by Bates & Harrison (1997): greatest length of skull including incisors (GTLi); condylo-canine length (CCL); zygomatic width (ZW); breadth of the cranium measured between the mastoids (MAB); breadth of braincase (BB); minimum width of postorbital constriction (POC); height of the skull (SKH); maxillary toothrow length (CM³); width across the upper molars (M³-M³); width across the upper canines (C¹-C¹); length of upper molar toothrow (M¹-M³); mandible length, including incisors (MLi); mandibular toothrow length (CM₃) and height of the coronoid process (COH). We traced the outline of the right wing of the adult female on a paper sheet with 10 x 10 mm grids before *rigor mortis* was achieved and subsequently analysed a digital scan of the tracing using Image J (Schneider *et al.*, 2012). We measured total area, hand wing area and arm wing area thrice and took the mean to reduce error in our measurements. Length measurements (wingspan, hand wing length and arm wing length) were measured only once. From the wing tracing, we calculated wing loading, aspect ratio and tip-shape index for the adult female individual following Norberg & Rayner (1987). Echolocation calls of free flying bats were recorded at the sampling site with an Anabat Walkabout detector (Titley Scientific, Brendale, Australia) with the microphone pointing towards the tunnel-like structure formed by the bamboo thicket. Calls were recorded just prior to the capture of two *E. denticulus* in the mist net. The recordings were analysed on Raven Pro 1.5.0 (Cornell Lab of Ornithology, Ithaca, USA) and statistics derived from 20 pulses representing search phase calls (i.e. with short terminal narrowband FM tails). Call parameters included start frequency (highest frequency, SF), end frequency (lowest frequency, EF), peak frequency with maximal energy (PF), bandwidth (BW) and duration (D) and were measured from a spectrogram of FFT size 1024 and a Hanning window.

To confirm species identification and further compare genetically the Indian specimens with other available

Disk-footed bats, we extracted DNA from an ethanol-preserved tissue sample from the adult female from Meghalaya (ZSI VMERS 621), and from two further *E. denticulus* specimens collected in Bu Gia Map NP, southern Vietnam (ZMMU S-184645 and S-184651; Kruskop, 2010). We also extracted DNA from a range of various other Vespertilionidae and Miniopteridae outgroups (Table 1). Whole DNA was extracted with the DNAeasy Blood and Tissue Kit (QIAGEN) following manufacturer's instructions and eluted in a final volume of 60 to 200 µl of TE buffer. We either amplified the whole mitochondrial cytochrome *b* gene with standard procedures (detailed e.g. in Sedlock *et al.*, 2020) or a shorter fragment of 421 bp with the primer pair mcb398 and mcb869, as described in Verma & Singh (2003). The PCR products were purified with exonuclease-I and shrimp alkaline phosphatase (Thermo Scientific Inc.) and sequenced with Sanger technology in both directions, using the same amplification primers. Chromatograms of the sequenced fragments were inspected visually to ensure that they did not contain double peaks or stop codons reminiscent of pseudogenes and were then aligned with the program Sequencher 4.8 (Gene Codes, Co). All new sequences were deposited in the GenBank (accession numbers MW491233 - MW491242).

To place the sequenced Disk-footed bats in a phylogenetic framework, we further downloaded from the GenBank a set of homologous sequences (see Table 1) representing a collection of Asian Myotinae, including all known *Submyotodon* species, five members of the closely related Kerivoulinae - Murininae, and other unrelated vespertilionids bearing more or less developed thumb or wrist pads (Csorba *et al.*, 2015). The aligned sequences were submitted to a maximum likelihood phylogenetic reconstruction with the program IQ-TREE v2.1.2 (Nguyen *et al.*, 2015). We used a fully partitioned model with three codon positions and the most appropriate substitution model for each partition, as identified by ModelFinder (Kalyaanamoorthy *et al.*, 2017). Branch support for this approach was evaluated with 1000 Ultrafast bootstraps (Hoang *et al.*, 2018). Similarly, Bayesian phylogenetic reconstruction were also performed on the same data set with a fully partitioned model, using MrBayes v3.2.7 (Ronquist *et al.*, 2012). Four independent MCMC chains were run for four million generations, sampling trees every thousand generation. Posterior probability support of nodes from the final consensus tree was obtained by removing the initial 10 K trees as burn-in.

RESULTS AND DISCUSSION

Description of the new Indian specimens

The two captured Disk-footed bats, one adult female (FA 33.5 mm) and another juvenile female (FA 33.9 mm) were netted in a forest patch dominated by bamboo thicket. They were recognized as *Eudiscopus denticulus*

(Osgood, 1932) owing to a combination of small size, conspicuous disk-like pads present on their feet and a *Myotis*-like tragus shape (Fig. 1). There were remarkable differences in pelage colour between the juvenile and adult individuals, the former (Fig. 1C) being much darker than the latter (Fig. 1A and B). The adult female had a bright reddish-brown pelage, except for the belly which was darker with paler tips. The individual hairs had darker roots both dorsally and ventrally. This colouration is thus brighter reddish brown as against cinnamon brown given in the original description of the species from Laos (Osgood, 1932) or to specimens from Vietnam (e.g. Kruskop, 2013). However, as noted by Koopman (1972) the Myanmar specimens were smaller and brighter than Laos specimens and our Meghalaya specimen thus resembles the Myanmar material in pelage colour and shorter forearm (Table 2). The wing membrane was dark brown and essentially devoid of hairs and joined at the base of the outer toe. The tail tip was completely enclosed within the interfemoral membrane which was little lighter in colour and slightly whitish on the underside. The muzzle was pinkish. The ears were relatively large and pointed, unlike those of e.g. *Tylonycteris* or *Glischropus*, whereas the tragus was straight with a concave outer border and blunt tip, much like that of a small *Myotis*. The thumbs were short (1.5 mm) and there were callosities at the thumb base which were dark pigmented and not very obvious. Schliemann & Rehn (1980) noted that these poorly differentiated thumb pads unlikely have adhesive function in *Eudiscopus*, unlike in *Tylonycteris* or *Glischropus*. Noticeable planter pads existed in the form of sub-rectangular adhesive discs (4 x 2.9 mm) which were dark pink in colour (Fig. 1B) and turning beige in ethanol-preserved specimens. This disc development was more pronounced than in *Tylonycteris* as noted by Schliemann & Hoerber (1978). The juvenile individual (as determined from less knobby and evenly tapered phalangeal-metacarpal joints) was externally similar to the adult one in all respects except that the pelage was dark brown (Fig. 1C).

The skull was very broad and flat (Fig. 2A and B); however, unlike *Tylonycteris*, rostrum was longer and narrower. The zygomatic arches were widely flared (ZW 9.7 mm). The coronoid process of mandible was high and blunt with concave posterior border (Fig. 2C). The upper incisors were bicuspid and similar in height and separated from the canine by a small gap. The canine was unicuspid and considerably exceeded the length of the third premolar. There were three pairs of lower premolars, the middle one (p₃) being minute and completely displaced internally. In our specimen, the anterior teeth of the mandible were shed during the chemical cleaning process but not before being able to examine the dental structure. Lower molars were all myotodont, as in most *Myotis* or *Tylonycteris*, but unlike in *Glischropus* (Kruskop, 2013).

Table 1. Species sampling for the molecular reconstructions based on the mitochondrial cytochrome *b* gene with corresponding museum voucher (if any), country of origin, GenBank entries and reference of the published sequences.

| Species | Voucher | Origin | GenBank | Reference |
|---------------------------------|-----------------|-------------|----------|---------------------------------|
| <i>Eudiscopus denticulus</i> | ZMMU S-184645 | Vietnam | MW491233 | This study |
| <i>Eudiscopus denticulus</i> | ZMMU S-184651 | Vietnam | MW491234 | This study |
| <i>Eudiscopus denticulus</i> | ZSI VMERS 621 | NE India | MW491242 | This study |
| <i>Glischropus aquilus</i> | MZB 35030 | Indonesia | KR612333 | Csorba <i>et al.</i> (2015) |
| <i>Glischropus bucephalus</i> | HNHM 2006.34.45 | Cambodia | KR612332 | Csorba <i>et al.</i> (2015) |
| <i>Glischropus bucephalus</i> | HNHM 21735 | Cambodia | MW491235 | This study |
| <i>Glischropus bucephalus</i> | HNHM 21736 | Cambodia | MW491236 | This study |
| <i>Glischropus tylopus</i> | MHNG 1970.063 | Malaysia | JX570898 | Heaney <i>et al.</i> (2012) |
| <i>Hesperoptenus blanfordi</i> | CPV10x40 | Cambodia | MF038482 | Hassanin <i>et al.</i> (2018) |
| <i>Hesperoptenus blanfordi</i> | MHNG 1970.053 | Malaysia | MW491237 | This study |
| <i>Hesperoptenus tickelli</i> | CPV10x21 | Cambodia | MF038483 | Hassanin <i>et al.</i> (2018) |
| <i>Kerivoula kachinensis</i> | ZSI VMERS 571 | NE India | JQ044697 | Ruedi <i>et al.</i> (2012) |
| <i>Kerivoula whiteheadi</i> | FMNH 177475 | Philippines | MG194438 | Sedlock <i>et al.</i> (2020) |
| <i>Miniopterus fuliginosus</i> | ZSI M2262 | NW India | MW054886 | Ruedi <i>et al.</i> (2021) |
| <i>Miniopterus magnater</i> | MHNG 1981.071 | NE India | MW054887 | Ruedi <i>et al.</i> (2021) |
| <i>Miniopterus medius</i> | MHNG 1970.051 | Malaysia | MW491238 | This study |
| <i>Miniopterus pusillus</i> | ZSI VMERS 570 | NE India | MW054888 | Ruedi <i>et al.</i> (2021) |
| <i>Murina cyclotis</i> | MHNG 1981.072 | NE India | JQ044691 | Ruedi <i>et al.</i> (2012) |
| <i>Murina pluvialis</i> | ZSI VMERS 603 | NE India | JQ044689 | Ruedi <i>et al.</i> (2012) |
| <i>Myotis alticraniatus</i> | MHNG 1956.090 | Laos | KF312531 | Ruedi <i>et al.</i> (2013) |
| <i>Myotis annamiticus</i> | ZMMU S-167134 | Vietnam | KF312499 | Ruedi <i>et al.</i> (2013) |
| <i>Myotis annatessae</i> | MHNG 1926.044 | Laos | KF312514 | Ruedi <i>et al.</i> (2013) |
| <i>Myotis cf. ater</i> | MHNG 1926.036 | Laos | KF312509 | Ruedi <i>et al.</i> (2013) |
| <i>Myotis blythii</i> | ZSI VMERS 405 | NW India | MW054872 | Ruedi <i>et al.</i> (2021) |
| <i>Myotis brandtii</i> | - | Asia | KM199849 | Jiang <i>et al.</i> (2016) |
| <i>Myotis davidii</i> | KM 13093 | S Korea | AY665148 | Tsytulina <i>et al.</i> (2012) |
| <i>Myotis fimbriatus</i> | HNHM 25872 | S China | MW054893 | Ruedi <i>et al.</i> (2021) |
| <i>Myotis horsfieldii</i> | ZMMU S-165039 | Vietnam | MW491239 | This study |
| <i>Myotis ikonnikovii</i> | - | S Korea | KF111724 | Yoon <i>et al.</i> (2015) |
| <i>Myotis longipes</i> | ZSI M2210 | NW India | MW054878 | Ruedi <i>et al.</i> (2021) |
| <i>Myotis mystacinus</i> | MHNG 3003.057 | Europe | MW054880 | Ruedi <i>et al.</i> (2021) |
| <i>Myotis nipalensis</i> | CDZTU B9 | Nepal | MW054894 | Ruedi <i>et al.</i> (2021) |
| <i>Myotis phanluongi</i> | ZMMU S-175154 | Vietnam | KF312525 | Ruedi <i>et al.</i> (2013) |
| <i>Myotis rosseti</i> | ROM 110487 | Laos | KF312527 | Ruedi <i>et al.</i> (2013) |
| <i>Myotis rosseti</i> | ZMMU S-175291 | Vietnam | MW491240 | This study |
| <i>Myotis sibiricus</i> | Mbra26RU | C Russia | MG897530 | Kocacova <i>et al.</i> (2018) |
| <i>Myotis siligorensis</i> | ZSI VMERS 601 | NE India | MW054883 | Ruedi <i>et al.</i> (2021) |
| <i>Phoniscus jagorii</i> | FMNH 202818 | Philippines | MG194467 | Sedlock <i>et al.</i> (2020) |
| <i>Scotozous dormeri</i> | MHNG 1947.073 | S India | MW491241 | This study |
| <i>Submyotodon caliginosus</i> | ZSI VMERS 421 | NW India | MW054884 | Ruedi <i>et al.</i> (2021) |
| <i>Submyotodon latirostris</i> | M608 | Taiwan | AM262330 | Stadelmann <i>et al.</i> (2007) |
| <i>Submyotodon moupinensis</i> | HNHM 26564 | S China | MW054895 | Ruedi <i>et al.</i> (2021) |
| <i>Tylonycteris fulvida</i> | MHNG 1926.055 | Laos | KX496526 | Tu <i>et al.</i> (2017) |
| <i>Tylonycteris malayana</i> | CPV10-503 | Cambodia | KX496369 | Tu <i>et al.</i> (2017) |
| <i>Tylonycteris tonkinensis</i> | MHNG 1926.059 | Laos | KX496441 | Tu <i>et al.</i> (2017) |

Table 2. Comparative measurements of the two *E. denticulus* from Meghalaya and 18 other individuals from Southeast Asia. External measurements were taken from both Meghalaya individuals, while only the adult female was measured for craniodental characters. Values in brackets are means.

| Measurements (in mm) | Meghalaya (n = 2) | Type from Laos (n = 1) | SE Asia (n = 18) |
|--------------------------------|----------------------|---------------------------|---------------------|
| W (g) | 3, 5 | - | 4.5-5.0 (4.8) |
| HB | 36.5, 40 | 43 | 35.9-40.5 (38) |
| TL | 37, 38 | 40 | 34.9-41.2 (38.6) |
| HF | 6.8 | 6.2 | 5.8-7.2 (6.6) |
| TB | 15.5 | 17.2 | 15.4-16.9 (16.3) |
| E | 11.5, 11.7 | - | 10.9-12.5 (11.6) |
| TR | 4.7, 5.2 | - | 5.6-5.9 (5.7) |
| FA | 33.5, 33.9 | 37.8 | 33.5-36.6 (34.5) |
| 3mt | 32 | 34.2 | 31.3-33.2 (32.3) |
| 4mt | 31.3 | 32.6 | 30.4-32.0 (31.0) |
| 5mt | 31.2 | 32.2 | 30.4-32.4 (31.3) |
| GTLi | 14.00 | 14.2 | 13.43-14.49 (13.99) |
| CCL | 12.50 | 13.2 | 12.15-13.16 (12.75) |
| ZW | 9.58 | 9.7 | 8.97-9.43 (9.21) |
| MAB | 7.52 | 7.7 | 7.20-7.81 (7.51) |
| BB | 6.70 | 7.0 | 6.36-6.99 (6.72) |
| POC | 3.77 | 3.6 | 3.40-3.94 (3.61) |
| SKH | 3.94 | 3.5 | 3.07-3.97 (3.67) |
| CM ³ | 5.11 | 5.4 | 5.20-5.49 (5.35) |
| M ³ -M ³ | 5.60 | 5.8 | 5.74-6.05 (5.83) |
| C ¹ -C ¹ | 3.62 | 3.8 | 3.59-3.91 (3.71) |
| M ¹ -M ³ | 3.61 | - | - |
| MLi | 10.10 | 10.6 | 9.74-10.63 (10.20) |
| CM ₃ | 5.28 | 5.5 | 5.49-5.85 (5.68) |
| COH | 3.26 | - | 3.00-3.38 (3.15) |

Revised distribution

So far, the species was reported from several localities in Southeast Asia *i.e.* Yetho River, Pegu Yoma in central Myanmar (Koopman, 1970); Khlong Lan National Park, Loei, Ratchaburi, and Surat Thani in Thailand (Schliemann & Kock, 2000; Soisook *et al.*, 2016), and Chu Mom Ray in Kon Tum Province in central, Cat Tien National Park in the south and Pu Huong, and Bu Gia Map Nature Reserve in north-central Vietnam (Borissenko & Kruskop 2003; Zsebök *et al.*, 2014; Kruskop, 2013, 2017). Very recently, it has also been reported from three localities in Yunnan Province of China (Yu *et al.*, 2021). According to Koopman (1970, 1972), the precise locality of two specimens from Myanmar housed in the AMNH *i.e.* “Yetho River, Pegu Yoma, 100ft” is indeterminate. This was confirmed by Schliemann & Kock (2000) who also noted that within a radius of 100 km, there are at least three low-elevation localities (under 50 m

a.s.l.) named “Yetho” in the slopes of Pegu mountains in Myanmar and one of these places might represent the source of the Myanmar’s specimens. In our view also, this locality represents a tributary of Sittuang river in south-central Myanmar and lies in the same general area (18° 00’ - 18° 05’N, 96° 00’ - 96° 05’E) as postulated by Schliemann & Kock (2000) and was hitherto considered the westernmost locality for this species. The present locality in Meghalaya thus represents a range extension of about 1000 km further west into the Indian Subcontinent (Fig. 3) and was not predicted to occur in this region according to the MaxEnt modelling study of Yu *et al.* (2021). Furthermore, except for the type locality which is situated at an altitude of about 1300 m a.s.l. in northern Laos (Schliemann & Rehn, 1980), all records of Disk-footed bats lie below 1000 m a.s.l., including the present record from north-eastern India (210 m a.s.l.), suggesting that this is a predominantly lowland species.

Ecological notes

The two Meghalaya Disk footed bats were caught in a net set at one of the entrances of a tunnel-like closed canopy forest with predominant bamboo growths (*Dendrocalamus* and *Bambusa* spp.). The general forest habitats found in the area belongs to Tropical semi-evergreen type (Champion & Seth, 1968). These bats were caught on the inner side of the net indicating they were emerging from inside the forest patch. By virtue of remarkable morphological features like a flattened skull and adhesive pads, these bats can roost inside cramped space clinging to smooth surfaces like bamboo internodes (Koopman, 1972; Kock & Kovac, 2000; Schliemann & Kock, 2000). Considering the bamboo-dominated forest from where these specimens were collected, a similar roosting preference can be expected in Meghalaya. A knowledgeable villager indicated occasional presence of bats inside bamboo internodes. However, he indicated that they were not as bright in colouration, possibly referring to other bamboo-dwelling bats (*Tylonycteris* spp.) which were also recorded by the senior author from the nearby Nongkhylliem WLS during bat surveys conducted in 2016. This indicates uncommon occurrence of *Eudiscopus* in the area. Similar observations were

also reported by Kock & Kovac (2000) who found *E. denticulus* only once in Thailand, after numerous probing in bamboo internodes in Southeast Asia, whereas *Tylonycteris* spp. were frequently recorded.

Echolocation

The echolocation call parameters (mean \pm standard deviation) were as follows: SF = 104.82 ± 2.7 kHz, EF = 53.12 ± 5.79 kHz, PF = 56.81 ± 2.86 kHz, BW = 51.69 ± 2.55 kHz and D = 4.75 ± 0.63 ms. These parameters and the entire call structure (Fig. 4) are similar to those previously recorded for *E. denticulus* (Hughes *et al.*, 2011; Zsebök *et al.*, 2014). Although we could not completely rule out the possibility of these recorded calls belonging to another species, it is most probable that the calls belong to *E. denticulus*. During the three hours of netting session at the site, the only other species caught were *Rhinolophus affinis* (emitting very distinct, constant-frequency signals) and *Pipistrellus coromandra*. Considering the rhythm and frequency range of the recorded calls which are much higher than those reported for *P. coromandra* elsewhere (Srinivasulu *et al.*, 2017), we can exclude confusion with this species



Fig. 1. Lateral (A) and frontal (B) view of an adult female (ZSIS 621) and lateral view (C) of juvenile (ZSIS 622) *E. denticulus* specimen from Meghalaya (images not to scale). Notice prominent pinkish plantar disc on the hind feet (image B).

as well. We did not record the long, upward-sweeping “unique call type” described by Zsebök *et al.* (2014) for *E. denticulus*. However, we recorded prominent hook-shaped starts in two pulses (as seen in some *Kerivoula* and *Murina* spp.; Schmieider *et al.*, 2010) that were not mentioned earlier (Fig. 4).

Wing morphology

Wing morphology and echolocation calls are a reliable method to assign guild membership to bats (Norberg & Rayner, 1987; Denzinger & Schnitzler, 2013) and also allow to predict the potential vulnerability of species to anthropogenic disturbance (Núñez *et al.*, 2019). However, these data are mostly lacking for tropical bat species, particularly those rare species like *E. denticulus*. Based on measurement of the adult female caught in Meghalaya, the moderate aspect ratio (6.64) and low wing loading (5.55) coupled with relatively broad tips (Tip-shape index = 1.68) indicate low flight speed and improved manoeuvrability (Norberg & Rayner, 1987). On account of these novel wing morphology data and relatively high echolocation call frequency, we corroborate Zsebök *et al.* (2014)’s guild assignment of *E. denticulus* as an ‘edge

space aerial forager’ (Denzinger & Schnitzler, 2013) that can adapt to a fair degree of clutter (as bamboo forests in this case). With such wing and echolocation call characteristics it appears less well adapted to forage in complete open space. We indeed observed the flight of the juvenile individual inside a large room performing a slow, fluttering flight similar to those of some *Pipistrellus* spp.

Genetics

The partial cytochrome *b* gene was successfully amplified and sequenced from the adult female *E. denticulus* from Meghalaya. Remarkably, the 421 aligned base pairs of this individual were identical to homologous sequences of *E. denticulus* from Vietnam, despite the over 2000 km straight distance separating the two sampling localities. Both individuals from Vietnam sequenced for the complete cytochrome *b* (1140 bp) were also nearly identical, with a single T/C transition noted in position 996. The comparison of various individuals sequenced for another mitochondrial gene (the cytochrome c oxidase subunit I) likewise suggest minimal (<1%) molecular variation in Disk-footed bats issued from distant places in

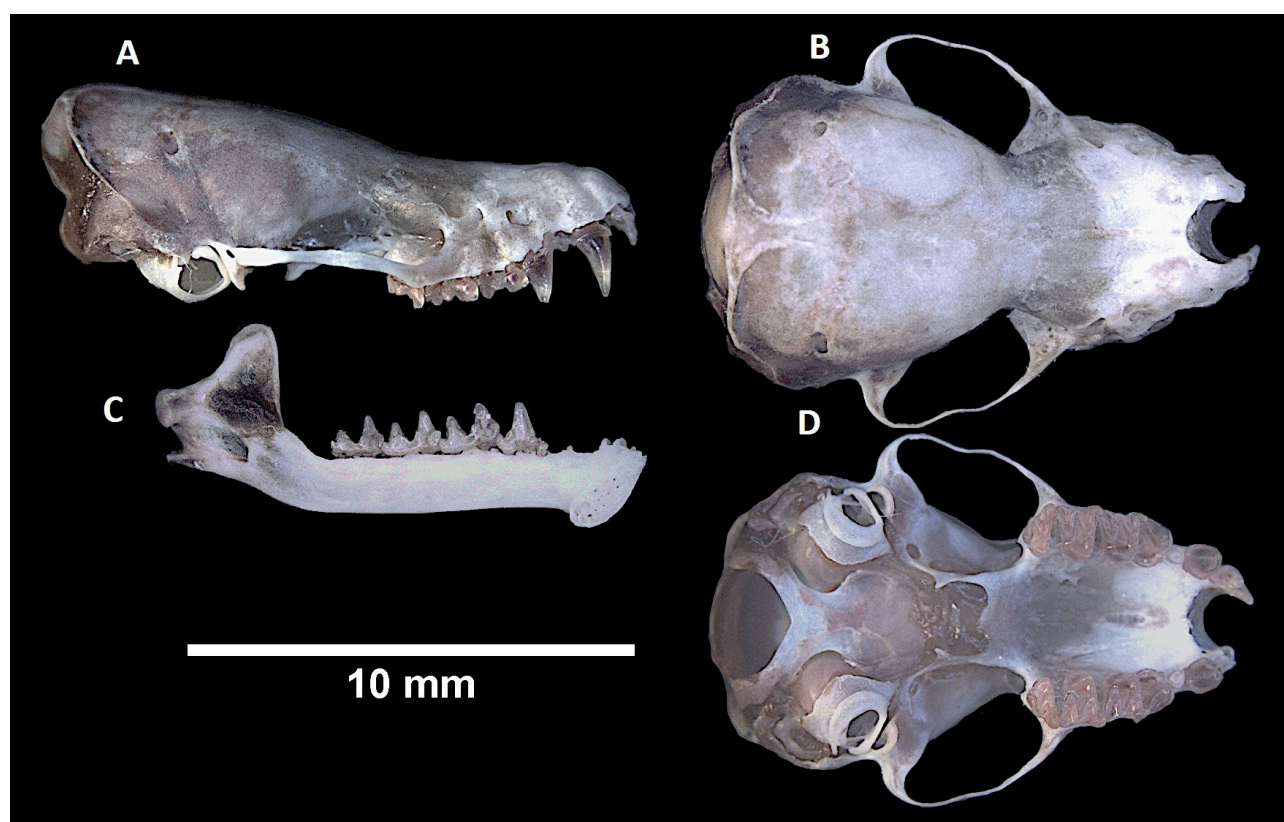


Fig. 2. Lateral (A), dorsal (B), ventral (D) view of cranium and of mandible (C) of ZSIS 621 specimen. Note that the mandibular dentition is incomplete due to inadvertent loss of few anterior teeth (incisors and canines) during the cleaning process of the skull.

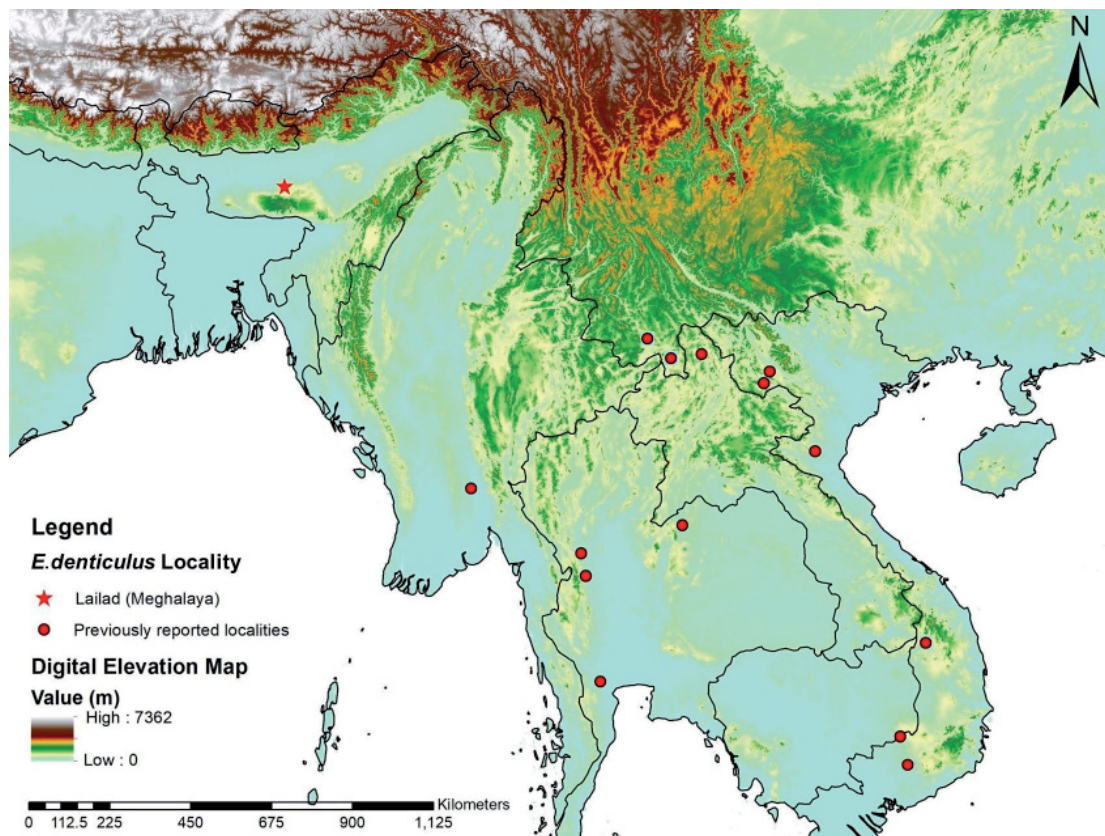


Fig. 3. Location of currently known records of *E. denticulus* in South and Southeast Asia.

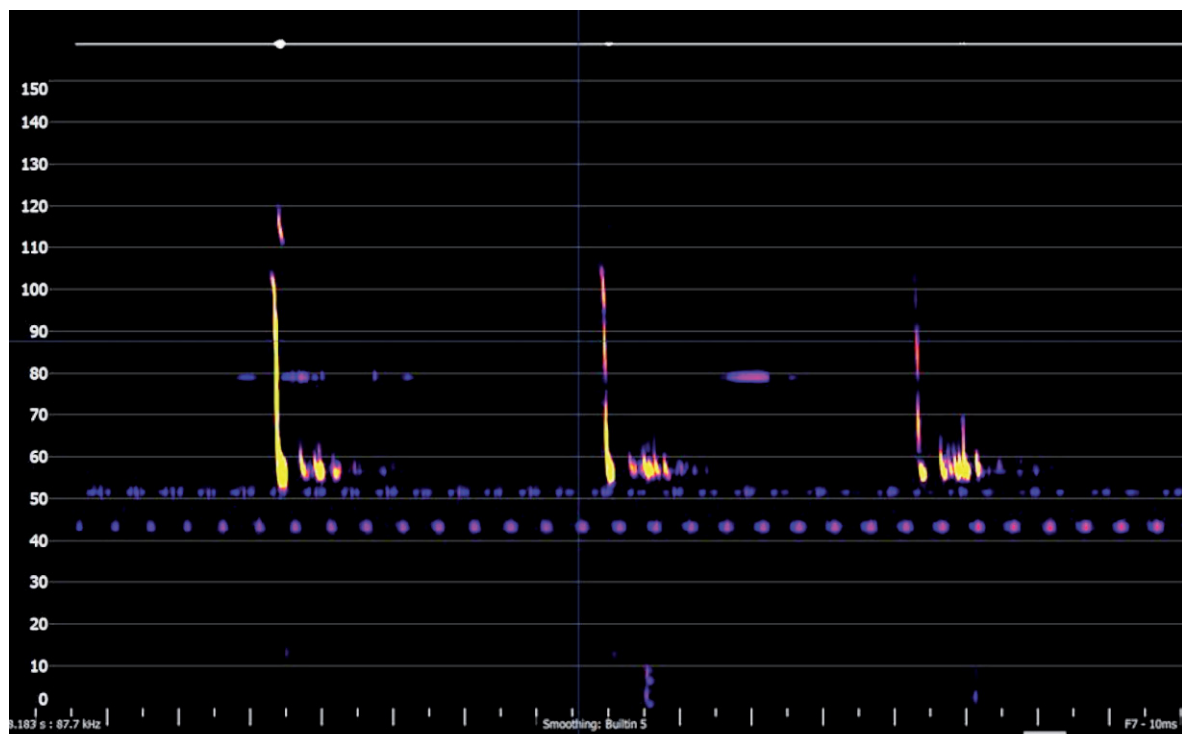


Fig. 4. Call spectrogram of a free flying individual of *E. denticulus* from Meghalaya. The values in the vertical axis indicate call frequency in kHz. Each division of the horizontal axis indicates a time interval of 10 milliseconds.

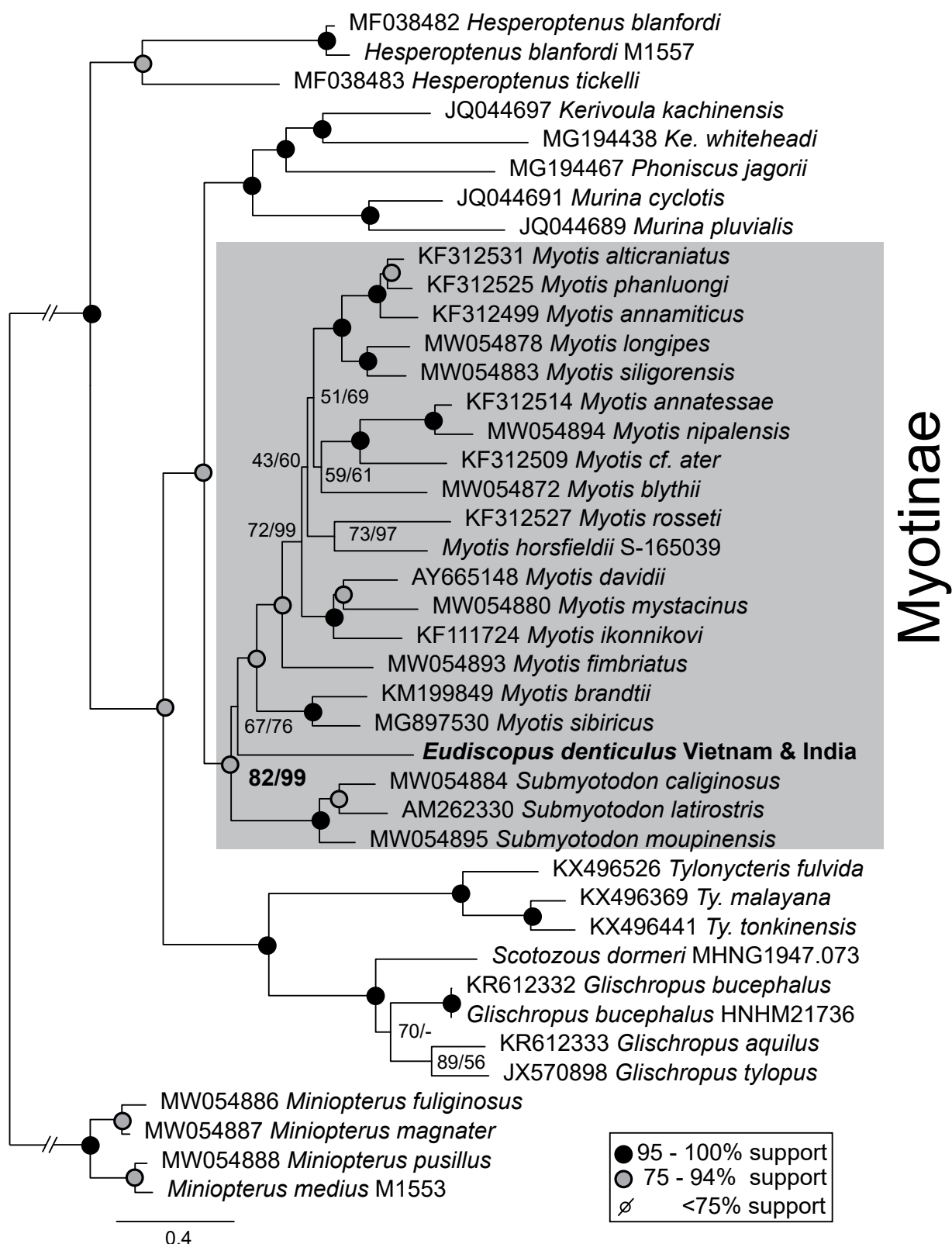


Fig. 5. Maximum likelihood reconstruction of the *Eudiscopus denticulus* lineage within a selection of Vespertilionidae and outgroup Miniopteridae bats. Percent nodal support obtained from 1000 Ultrafast repeats in iQ-tree and posterior probabilities in MrBayes are indicated at each node. The actual percentages are given near each node which received less than 75% support, whereas shades of grey are used when both reconstruction methods retrieved higher support for the same node. The newly sequenced *M. rosseti* (ZMMU S-175291) and *G. bucephalus* (HMNH 21735) are not represented here, as they were identical to conspecifics.

Vietnam (Kruskop *et al.*, unpublished 2018) or in Yunnan, China (Yu *et al.*, 2021). Such high genetic similarities for mitochondrial genes characterized by relatively high mutation rates in mammals, including bats (Bradley & Baker, 2001) suggest that *Eudiscopus* populations from Vietnam, China and Meghalaya certainly have a very recent common origin. As secondary bamboo regrowth has been greatly favoured by the adoption of slash-and-burn culture by expanding human population in Indochina, one hypothesis would be that these bat populations expanded from the same region, following the very recent expansion of man-made bamboo groves. Compared to other cytochrome *b* from various bat species (Table 1), these sequences of *E. denticulus* differ by at least 18% Kimura-two-parameter distance from any other *Myotis* or *Submyotodon* tested, and by 19% or more from other Vespertilionidae. All phylogenetic reconstructions based on this gene were very concordant and clearly placed the single *Eudiscopus* lineage within the Myotinae, with 82 (maximum likelihood) to 99% (Bayesian) support (Fig. 5). Unfortunately, these reconstructions could not resolve the relative position of *Eudiscopus* in this radiation, as the other two Myotinae, *Myotis* and *Submyotodon*, were also placed near the base of this radiation with low nodal support. A basal position of *Eudiscopus* within the Myotinae corroborate previous molecular reconstructions based on a small selection of Vespertilionidae and the 12S rDNA sequences (Borisenko *et al.*, 2008). The recent and more extensive sampling of the mitochondrial genome of several Vespertilionidae also concluded that *Eudiscopus* was the most basal Myotinae (Yu *et al.*, 2021), but clearly, genes from the nuclear genome are needed to completely resolve this radiation. At least, alternative phylogenetic hypotheses placing *Eudiscopus* with other bats bearing enlarged or disk-like pads (e.g. *Glischropus* spp., *Tylonycteris* spp., *Hesperoptenus* spp. or *Myotis rosseti*) or close to other Vespertilioninae can be clearly excluded by current molecular reconstructions.

Despite the relatively small geographic area of the state of Meghalaya, this discovery of a new genus in the country both confirm that this region is exceptionally rich in Chiropteran diversity, and certainly is still underexplored (Ruedi *et al.*, 2012). With the present addition of *E. denticulus* from Meghalaya, the reported bat diversity of the state has increased to 66 species and that of India to 130 species (Saikia, 2018; Saikia *et al.*, 2018; Chakravarty *et al.*, 2020; Ruedi *et al.*, 2021).

ACKNOWLEDGEMENTS

We are thankful to Dr Kailash Chandra, Director, Zoological Survey of India, Kolkata for support and institutional facilities. We also appreciate manifold assistances from Sh. H. C. Choudhary, Chief Wildlife Warden, Govt of Meghalaya and the Divisional Forest

Officer, East Khasi Hills (Wildlife) Division. Laboratory and cartographic assistance from Dr Abhijit Das and Bitupon Barua are also greatly appreciated. U.S. thanks colleagues in ZSI, Shillong for field assistance and Rudolf Haslauer, Poernbach, Germany for access to literature. The work of G.C. received support from the National Research, Development and Innovation Fund of Hungary NKFIH KH130360. The work of S.V.K. was performed in line with the ZMMU State theme (2021-2025). We appreciate the suggestions made by Tommy Andriollo and Vuong Tan Tu on an earlier version of this manuscript.

REFERENCES

- Amador L.I., Arevalo R.L.M., Almeida F.C., Catalano S.A., Giannini N.P. 2018. Bat systematics in the light of unconstrained analyses of a comprehensive molecular supermatrix. *Journal of Mammalian Evolution* 25: 37-70.
- Bates P.J.J., Harrison D.L. 1997. Bats of the Indian Subcontinent. *Harrison Zoological Museum, Sevenoaks, UK*, 258 pp.
- Borisenko A.V., Kruskop S.V. 2003. Bats of Vietnam and adjacent territories. An identification manual. *Moscow, Russia*, 203 pp.
- Borisenko A.V., Kruskop S.V., Ivanova N.V. 2008. A new mouse-eared bat (Mammalia: Chiroptera: Vespertilionidae) from Vietnam. *Russian Journal of Theriology* 7: 57-69.
- Bradley R., Baker R. 2001. A test of the genetic species concept: cytochrome *b* sequences and mammals. *Journal of Mammalogy* 82: 960-973.
- Champion H.G., Seth S.K. 1968. A revised survey of the forest types of India. *Manager of Publications, Government of India, New Delhi*, 404 pp.
- Chakravarty R., Ruedi M., Ishtiaq F. 2020. A recent survey of bats with descriptions of echolocation calls and new records from the western Himalayan region of Uttarakhand, India. *Acta Chiropterologica* 22: 197-224.
- Conisbee L.R. 1953. Genera and subgenera of recent mammals. *British Museum (Natural History), London, UK*, 109 pp.
- Csorba G., Görföl T., Wiantoro S., Kingston T., Bates P.J.J., Huang J.C.-C. 2015. Thumb-pads up: a new species of thick-thumbed bat from Sumatra (Chiroptera: Vespertilionidae: *Glischropus*). *Zootaxa* 3980: 267-278.
- Denzinger A., Schnitzler H.U. 2013. Bat guilds, a concept to classify the highly diverse foraging and echolocation behaviors of microchiropteran bats. *Frontiers in Physiology*: 1-15.
- Görföl T., Furey N.M., Bates P.J.J., Csorba G. 2019. The identity of '*Falsistrellus*' *affinis* from Myanmar and Cambodia and new records of *Hypsugo dolichodon* from these countries. *Acta Chiropterologica* 20: 301-309.
- Haslauer R. 2019. *Eudiscopus denticulus*. In: Wilson D. E., Mittermeier R. A. (eds). *Handbook of the Mammals of the World: Bats*. Vol. 9, *Lynx Edicions, Barcelona, Spain*, p. 923.
- Hassanin A., Colombo R., Gembu G.-C., Merle M., Tu V.T., Görföl T., Akawa P.M., Csorba G., Kearney T., Monadjem A., Ing R.K. 2018. Multilocus phylogeny and species delimitation within the genus *Glauconycteris* (Chiroptera, Vespertilionidae), with the description of a new bat species from the Tshopo Province of the Democratic Republic of

- the Congo. *Journal of Zoological Systematics and Evolutionary Research* 56: 1-22.
- Heaney L.R., Balete D.S., Alviola P., Rickart E.A., Ruedi M. 2012. *Nyctalus plancyi* and *Falsistrellus petersi* (Chiroptera: Vespertilionidae) from northern Luzon, Philippines: ecology, phylogeny, and biogeographic implications. *Acta Chiropterologica* 14: 265-278.
- Hoang D.T., Chernomor O., von Haeseler A., Minh B.Q., Vinh L.S. 2018. UFBoot2: Improving the ultrafast bootstrap approximation. *Molecular Biology and Evolution* 35: 518-522.
- Hughes A., Chutamas S., Bates P., Soisook P., Sritongchuay T., Jones G. 2011. Using echolocation calls to identify Thai bat species: Vespertilionidae, Emballonuridae, Nycteridae and Megadermatidae. *Acta Chiropterologica* 13: 447-455.
- Jiang J.-J., Wang S.-Q., Li Y.-J., Zhang W., Yin A.-G., Hu M. 2016. The complete mitochondrial genome of insect-eating Brandt's bat, *Myotis brandtii* (*Myotis*, Vespertilionidae). *Mitochondrial DNA* 27: 1403-1404.
- Kalyaanamoorthy S., Minh B.Q., Wong T.K.F., von Haeseler A., Jermini L.S. 2017. ModelFinder: fast model selection for accurate phylogenetic estimates. *Nature Methods* 14: 587-589.
- Kock D., Kovac D. 2000. *Eudiscopus denticulus* (Osgood, 1932) in Thailand with notes on its roost. *Zeitschrift für Säugetierkunde* 65: 121-123.
- Koopman K. 1970. A second locality for *Eudiscopus denticulus* (Chiroptera: Vespertilionidae). *Journal of Mammalogy* 51: 191.
- Koopman K. 1972. *Eudiscopus denticulus*. *Mammalian Species* 19: 1-2.
- Kovacova V., Zukal J., Bandouchova H., Botvinkin A.D., Harazim M., Martínková N., Orlov O.L., Piacek V., Shumkina A.P., Tiunov M.P., Pikula J. 2018. White-nose syndrome detected in bats over an extensive area of Russia. *BMC Veterinary Research* 14: 1-9.
- Kruskop S.V. 2010. Preliminary data on the bat fauna of Bu Gia Map National Park (southern Vietnam). *Plecotus et al.* 13: 69-74 [in Russian].
- 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 MV Lomonosov State University, Moscow*, 300 pp.
- Kruskop S.V. 2017. Between North and South: provisional data on bats (Mammalia: Chiroptera) from Gia Lai – Kon Tum plateaus. *Journal of Tropical Science and Technology* 14: 59-66
- Nguyen L.-T., Schmidt H.A., von Haeseler A., Minh B.Q. 2015. IQ-TREE: A fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Molecular Biology and Evolution* 32: 268-274.
- Norberg U.M., Rayner J.M.V. 1987. Ecological morphology and flight in bats (Mammalia; Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. *Philosophical Transactions of the Royal Society of London, Series B* 316: 335-427.
- Núñez S.F., López-Baucells A., Rocha R., Farneda F.Z., Bobrowiec P.E.D., Palmeirim J.M., Meyer C.F.J. 2019. Echolocation and stratum preference: key trait correlates of vulnerability of insectivorous bats to tropical forest fragmentation. *Frontiers in Ecology and Evolution* 7: 373.
- Osgood W.H. 1932. Mammals of the Kelley Roosevelt and Delacour Asiatic expeditions. *Field Museum of Natural History, Zoological Series*, 18: 193-339.
- Ronquist F., Teslenko M., Van Der Mark P., Ayres D.L., Darling A., Höhna S., Larget B., Liu L., Suchard M.A., Huelsenbeck J.P. 2012. MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61: 539-542.
- Ruedi M., Biswas J., Csorba G. 2012. Bats from the wet: two new species of Tube-nosed bats (Chiroptera: Vespertilionidae) from Meghalaya, India. *Revue suisse de Zoologie* 119: 111-135.
- Ruedi M., Stadelmann B., Gager Y., Douzery E.J.P., Francis C.M., Lin L.-K., Guillén-Servent A., Cibois A. 2013. Molecular phylogenetic reconstructions identify East Asia as the cradle for the evolution of the cosmopolitan genus *Myotis* (Mammalia, Chiroptera). *Molecular Phylogenetics and Evolution* 69: 437-449.
- Ruedi M., Saikia U., Thabah A., Görföl T., Thapa S., Csorba G. 2021. Molecular and morphological revision of small Myotinae from the Himalayas shed new light on the poorly known genus *Submyotodon* (Chiroptera: Vespertilionidae). *Mammalian Biology*. (in press)
- Saikia U. 2018. A review of chiropterological studies and a distributional list of the bat fauna of India. *Records of the Zoological Survey of India* 118: 242-280.
- Saikia U., Thabah A., Chachula O.M., Ruedi M. 2018. The bat fauna of Meghalaya, Northeast India: Diversity and Conservation. In: Sivaperuman & Venkataraman (eds), Indian Hotspots: Vertebrate faunal diversity, conservation and management. Vol 2. *Springer Nature Singapore Pvt Ltd.*, pp. 263-286.
- Schliemann H., Hoerber M. 1978. The structure and the function of the pads on the thumb and foot of *Tylonycteris*. *Proceedings of the 4th International Bat Research Conference, Nairobi*, p. 39.
- Schliemann H., Kock D. 2000. Notes on the rare vespertilionid bat *Eudiscopus denticulus* (Osgood, 1932) (Chiroptera, Vespertilioninae). *Mitteilungen aus den Hamburgischen Zoologischen Museum und Institut* 97: 131-134.
- Schliemann H., Rehn C. 1980. Zur Kenntnis der Haftorgane von *Eudiscopus denticulus* (Osgood, 1932) (Mammalia: Microchiroptera: Vespertilionidae). *Zeitschrift für Säugetierkunde* 45: 29-39.
- Schmieder D.A., Kingston T., Hashim R., Siemers B.M. 2010. Breaking the trade-off: rainforest bats maximize bandwidth and repetition rate of echolocation calls as they approach prey. *Biology Letters* 6: 604-609.
- Schneider C.A., Rasband W.S., Eliceiri K.W. 2012. NIH Image to ImageJ: 25 years of image analysis. *Nature Methods* 9: 671-675.
- Sedlock J.L., Heaney L.R., Balete D.S., Ruedi M. 2020. Philippine bats of the genus *Kerivoula* (Chiroptera: Vespertilionidae): Overview and assessment of variation in *K. pellucida* and *K. whiteheadi*. *Zootaxa* 4755: 454-490.
- Sikes R.S. et al. 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. *Journal of Mammalogy* 97: 663-688.
- Simmons N.B. 2005. Order Chiroptera (pp. 312-529). In: Wilson D. E., Reeder D. M. (eds), Mammal species of the world. A taxonomic and geographic reference. *Johns Hopkins University Press, Washington*, 3rd ed.
- Soisook P., Csorba G., Bumrungsri S., Francis C.M., Bates P., Kingston T. 2016. *Eudiscopus denticulus*. *The IUCN Red*

- List of Threatened Species* 2016: e.T8168A22028419. DOI: 10.2305/IUCN.UK.2016-2.RLTS.T8168A22028419.en. Downloaded on 10 July 2020.
- Srinivasulu C., Srinivasulu A., Srinivasulu B., Gopi A., Dar T. A., Bates P.J.J., Rossiter S., Jones G. 2017. Recent surveys of bats from Andaman Islands, India: Diversity, distribution and echolocation call characteristics. *Acta Chiropterologica* 19: 419-437.
- Stadelmann B., Kunz T.H., Lin L.K., Ruedi M. 2007. Molecular phylogeny of New World *Myotis* (Chiroptera, Vespertilionidae) inferred from mitochondrial and nuclear DNA genes. *Molecular Phylogenetics and Evolution* 43: 32-48.
- Tate G.H. 1942. Results of the Archbold expeditions, 47: a review of the vespertilionine bats. *Bulletin of the American Museum of Natural History* 80: 221-297.
- Tsytulina K., Kruskop S., Masuda R. 2007. Taxonomical position of genus *Eudiscopus* (Chiroptera, Mammalia) among vespertilionid bats. *Bat Research News* 44: 309.
- Tsytulina K., Dick M.H., Maeda K., Masuda R. 2012. Systematics and phylogeography of the steppe whiskered bat *Myotis aurascens* Kuzyakin, 1935 (Chiroptera, Vespertilionidae). *Russian Journal of Theriology* 11: 1-20.
- Tu V.T., Csorba G., Ruedi M., Furey N.M., Son N.T., Thong V.D., Bonillo C., Hassanin A. 2017. Comparative phylogeography of bamboo bats of the genus *Tylonycteris* (Chiroptera, Vespertilionidae) in Southeast Asia. *European Journal of Taxonomy* 274: 1-38.
- Verma S.K., Singh L. 2003. Novel universal primers establish identity of an enormous number of animal species for forensic application. *Molecular Ecology Notes* 3: 28-31.
- Yoon K.B., Cho J.Y., Park Y.C. 2015. Complete mitochondrial genome of the Korean Ikonnikov's bat *Myotis ikonnikovi* (Chiroptera: Vespertilionidae). *Mitochondrial DNA* 26: 274-275.
- Yu W., Wu Y., Yang G. 2014. Early diversification trend and Asian origin for extant bat lineages. *Journal of Evolutionary Biology* 27: 2204-2218.
- Yu W.-H., Csorba G., Huang Z.-L., Li Y.-N., Quan R.-C., Wang Q.-Y., Liu S., Shi H.-Y., Wu Y., Li S. 2021. The first record of the disc-footed bat *Eudiscopus denticulus* (Chiroptera, Vespertilionidae) from China and the resolution of the phylogenetic position of the genus. *Zoological Research* 42: 94-99.
- Zsebök S., Son N.T., Csorba G. 2014. Acoustic characteristics of the echolocation call of the disc-footed bat, *Eudiscopus denticulus* (Osgood, 1932) (Chiroptera, Vespertilionidae). *Acta Acoustica united with Acustica* 100: 767-771.