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

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

Uttam Saikia[1], Rohit Chakravarty[2], Vishwanath D. Hegde[1], Asem Bipin Meetei[1], Sergei Kruskop[3], Gabor Csorba[4] & 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 guilde 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.

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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; Görföl *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 Nongkhyllem 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 (CM^3); width across the upper molars (M^3-M^3); width across the upper canines (C^1-C^1); length of upper molar toothrow (M^1-M^3); mandible length, including incisors (MLi); mandibular toothrow length (CM_3) 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 & Hoeber (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 (p_3) 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
Eudiscopus denticulus	ZMMU S-184645	Vietnam	MW491233	This study
Eudiscopus denticulus	ZMMU S-184651	Vietnam	MW491234	This study
Eudiscopus denticulus	ZSI VMERS 621	NE India	MW491242	This study
Glischropus aquilus	MZB 35030	Indonesia	KR612333	Csorba *et al.* (2015)
Glischropus bucephalus	HNHM 2006.34.45	Cambodia	KR612332	Csorba *et al.* (2015)
Glischropus bucephalus	HNHM 21735	Cambodia	MW491235	This study
Glischropus bucephalus	HNHM 21736	Cambodia	MW491236	This study
Glischropus tylopus	MHNG 1970.063	Malaysia	JX570898	Heaney *et al.* (2012)
Hesperoptenus blanfordi	CPV10x40	Cambodia	MF038482	Hassanin *et al.* (2018)
Hesperoptenus blanfordi	MHNG 1970.053	Malaysia	MW491237	This study
Hesperoptenus tickelli	CPV10x21	Cambodia	MF038483	Hassanin *et al.* (2018)
Kerivoula kachinensis	ZSI VMERS 571	NE India	JQ044697	Ruedi *et al*. (2012)
Kerivoula whiteheadi	FMNH 177475	Philippines	MG194438	Sedlock *et al*. (2020)
Miniopterus fuliginosus	ZSI M2262	NW India	MW054886	Ruedi *et al*. (2021)
Miniopterus magnater	MHNG 1981.071	NE India	MW054887	Ruedi *et al*. (2021)
Miniopterus medius	MHNG 1970.051	Malaysia	MW491238	This study
Miniopterus pusillus	ZSI VMERS 570	NE India	MW054888	Ruedi *et al*. (2021)
Murina cyclotis	MHNG 1981.072	NE India	JQ044691	Ruedi *et al*. (2012)
Murina pluvialis	ZSI VMERS 603	NE India	JQ044689	Ruedi *et al*. (2012)
Myotis alticraniatus	MHNG 1956.090	Laos	KF312531	Ruedi *et al*. (2013)
Myotis annamiticus	ZMMU S-167134	Vietnam	KF312499	Ruedi *et al*. (2013)
Myotis annatessae	MHNG 1926.044	Laos	KF312514	Ruedi *et al*. (2013)
Myotis cf. *ater*	MHNG 1926.036	Laos	KF312509	Ruedi *et al*. (2013)
Myotis blythii	ZSI VMERS 405	NW India	MW054872	Ruedi *et al*. (2021)
Myotis brandtii	-	Asia	KM199849	Jiang *et al*. (2016)
Myotis davidii	KM 13093	S Korea	AY665148	Tsytsulina *et al*. (2012)
Myotis fimbriatus	HNHM 25872	S China	MW054893	Ruedi *et al*. (2021)
Myotis horsfieldii	ZMMU S-165039	Vietnam	MW491239	This study
Myotis ikonnikovi	-	S Korea	KF111724	Yoon *et al*. (2015)
Myotis longipes	ZSI M2210	NW India	MW054878	Ruedi *et al*. (2021)
Myotis mystacinus	MHNG 3003.057	Europe	MW054880	Ruedi *et al*. (2021)
Myotis nipalensis	CDZTU B9	Nepal	MW054894	Ruedi *et al*. (2021)
Myotis phanluongi	ZMMU S-175154	Vietnam	KF312525	Ruedi *et al*. (2013)
Myotis rosseti	ROM 110487	Laos	KF312527	Ruedi *et al*. (2013)
Myotis rosseti	ZMMU S-175291	Vietnam	MW491240	This study
Myotis sibiricus	Mbra26RU	C Russia	MG897530	Kocacova *et al*. (2018)
Myotis siligorensis	ZSI VMERS 601	NE India	MW054883	Ruedi *et al*. (2021)
Phoniscus jagorii	FMNH 202818	Philippines	MG194467	Sedlock *et al*. (2020)
Scotozous dormeri	MHNG 1947.073	S India	MW491241	This study
Submyotodon caliginosus	ZSI VMERS 421	NW India	MW054884	Ruedi *et al*. (2021)
Submyotodon latirostris	M608	Taiwan	AM262330	Stadelmann *et al*. (2007)
Submyotodon moupinensis	HNHM 26564	S China	MW054895	Ruedi *et al*. (2021)
Tylonycteris fulvida	MHNG 1926.055	Laos	KX496526	Tu *et al*. (2017)
Tylonycteris malayana	CPV10-503	Cambodia	KX496369	Tu *et al*. (2017)
Tylonycteris tonkinensis	MHNG 1926.059	Laos	KX496441	Tu *et al*. (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; Zsebők *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 Nongkhyllem 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 ± 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; Zsebők *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 Zsebők *et al*. (2014) for *E. denticulus*. However, we recorded prominent hook-shaped starts in two pulses (as seen in some *Kerivoula* and *Murina* spp.; Schmieder *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 Zsebők *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

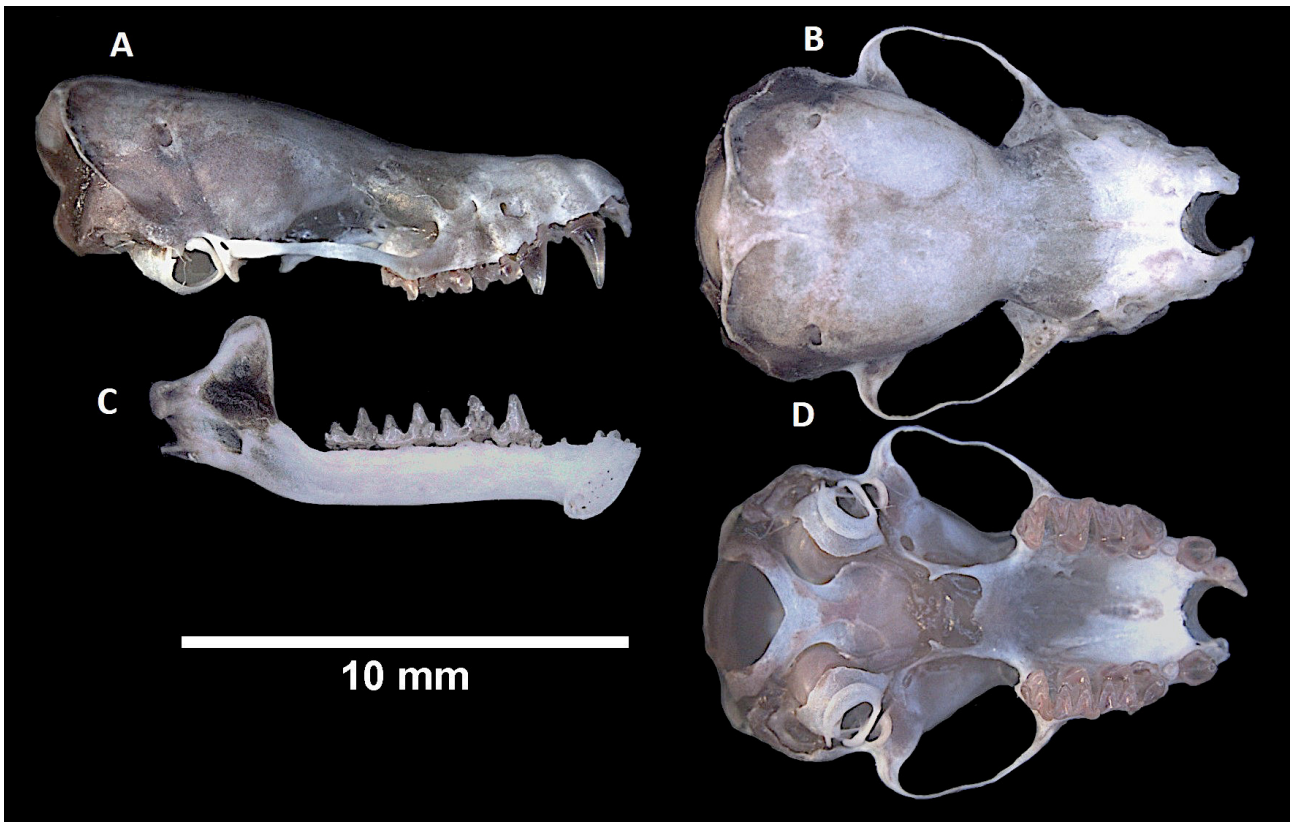

Fig. 2. Lateral (A), dorsal (B), ventral (D) view of cranium and of mandible (C) of ZSIS 621 specimen. Note that the mandibular dentition is incomplete due to inadvertent loss of few anterior teeth (incisors and canines) during the cleaning process of the skull.

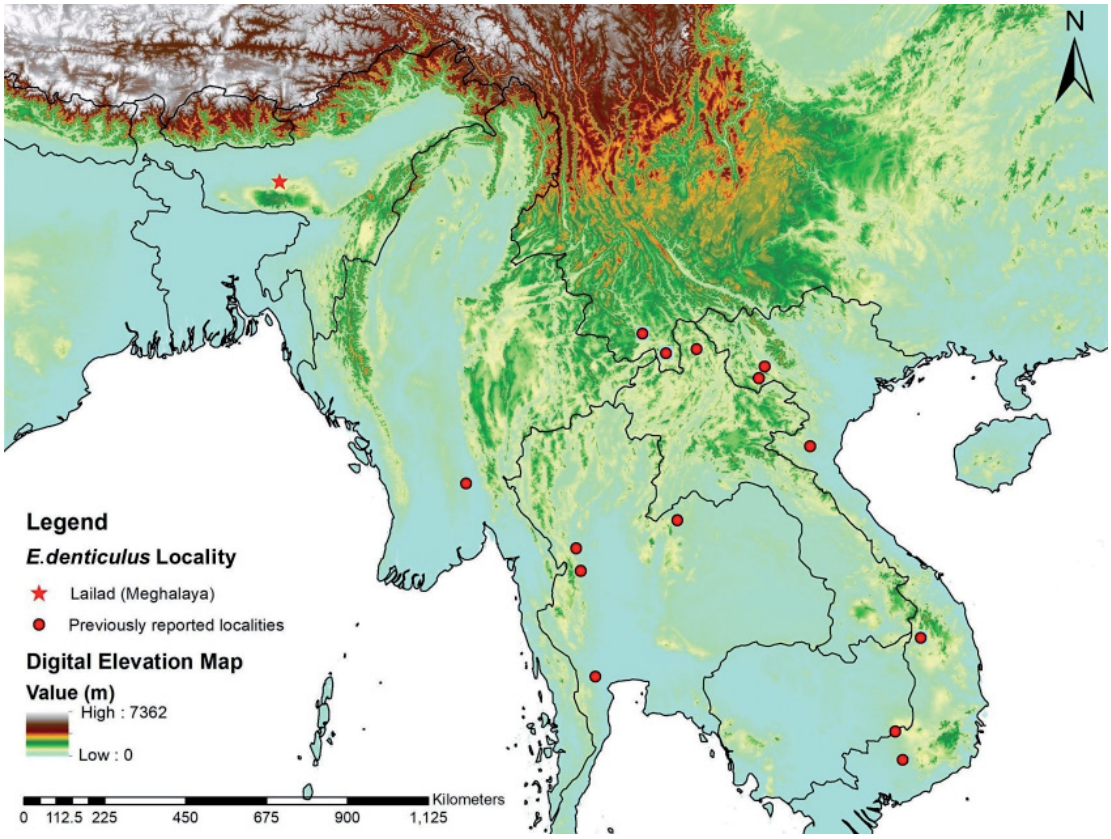

Fig. 3. Location of currently known records of *E. denticulus* in South and Southeast Asia.

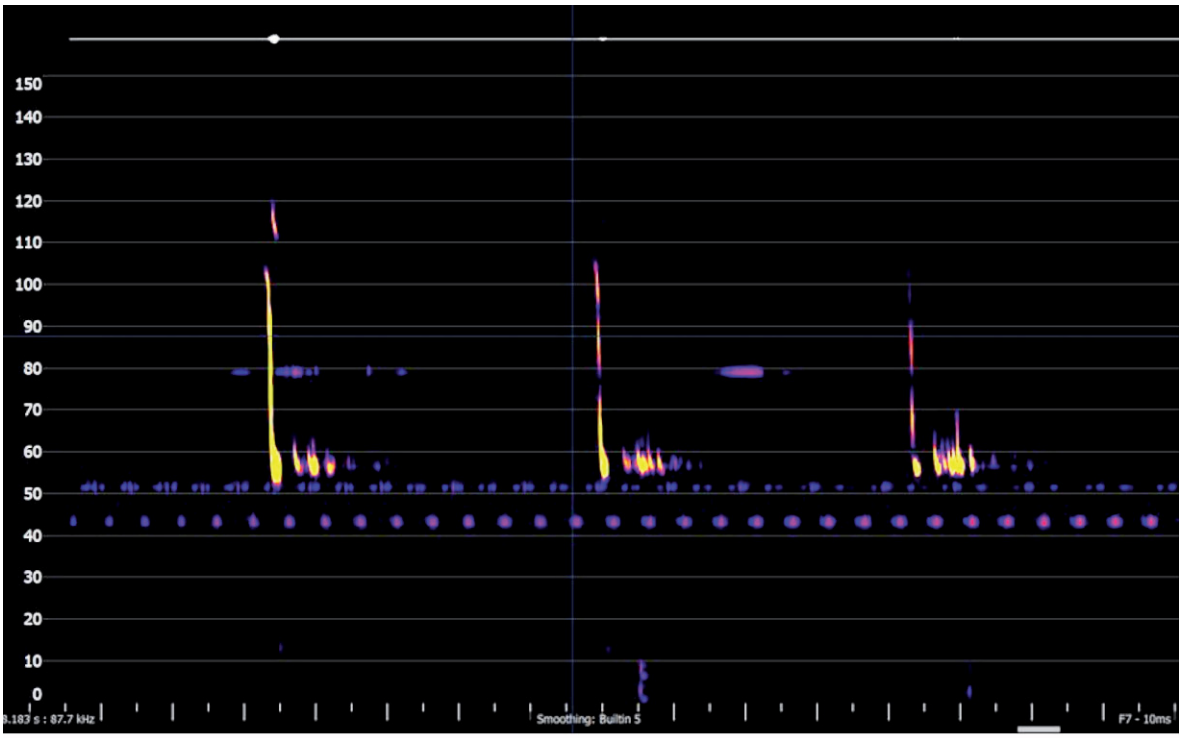

Fig. 4. Call spectrogram of a free flying individual of *E. denticulus* from Meghalaya. The values in the vertical axis indicate call frequency in kHz. Each division of the horizontal axis indicates a time interval of 10 milliseconds.

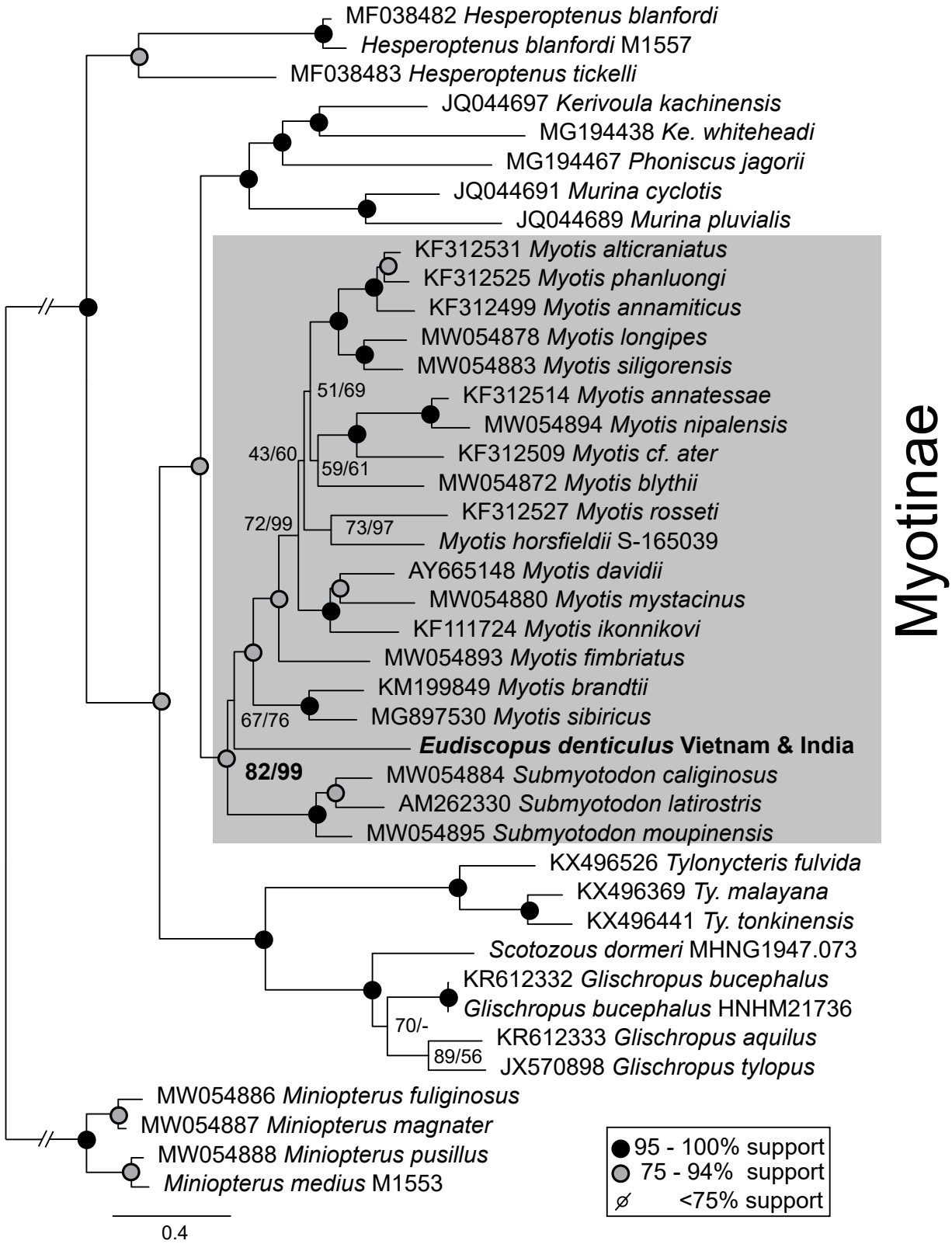

Fig. 5. Maximum likelihood reconstruction of the *Eudiscopus denticulus* lineage within a selection of Vespertilionidae and outgroup Miniopteridae bats. Percent nodal support obtained from 1000 Ultrafast repeats in iQ-tree and posterior probabilities in MrBayes are indicated at each node. The actual 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).

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