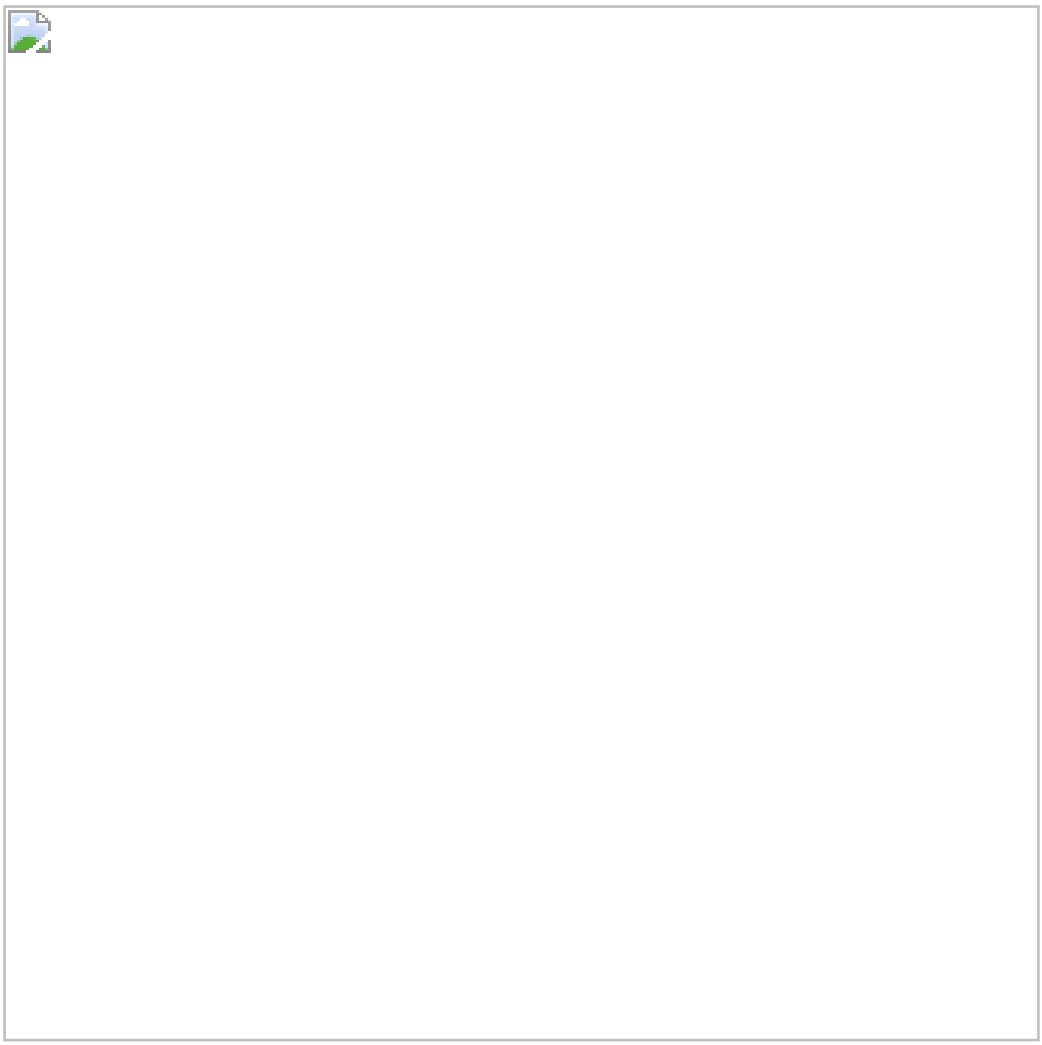

DNA Barcoding and Morphological Analyses Reveal a Cryptic Species of Miniopterus from India and Sri Lanka

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DNA barcoding and morphological analyses reveal a cryptic species of *Miniopterus* from India and Sri Lanka

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The genus *Miniopterus* is a monophyletic assemblage of many species characterized by remarkably conservative morphology. The number of recognized species has more than doubled over the last two decades, mainly with newly recognized Afrotropical and Malagasy species. A molecular phylogenetic analysis based on cytochrome *c* oxidase subunit I (*COI*) revealed a monophyletic clade of *Miniopterus* from Sri Lanka and southern India that is distinct from the other known taxa of this genus. The mean uncorrected pairwise sequence divergence among the three gene sequences of this new *Miniopterus* lineage was 0.83% (range 0.4–1.2%) and between this and other sampled taxa was 12.7% (range 8.5–15.9%). This lineage was also distinctive in craniodental morphometrics and hence it is herein described as a new species. The newly described species is easily distinguished by its external and cranial dimensions from its smaller (*M. pusillus*) and larger (*M. magnater*) congeners in India and Sri Lanka. It is also somewhat smaller than *M. fuliginosus* in both external and cranial dimensions. This is the first description of a new *Miniopterus* species from Asia in six decades and from India and Sri Lanka in eight decades. Our study highlights the importance of using both genetic and morphometric analyses in taxonomic studies on South Asian bats.

Key words: cryptic species, Miniopteridae, cytochrome oxidase 1, morphometrics, taxonomy, South Asia, DNA barcode

INTRODUCTION

The Old World bat genus *Miniopterus* Bonaparte, 1837, the sole representative of the family Miniopteridae, is characterized by remarkably conservative morphology and is considered as a monophyletic assemblage containing many cryptic species (Ramasindrazana *et al.*, 2011). As recently as 2005, the genus was thought to contain 19 species distributed over much of the Eastern Hemisphere (Simmons, 2005). However, recent descriptions has more than doubled that number (Ibáñez and Juste, 2019; Monadjem *et al.*, 2019, 2020), and additional putative species await confirmation (Demos *et al.*, 2020). Besides the genus *Murina* (which increased from 17 to 40 species since 2005 — Burgin *et al.*, 2020), no other speciose bat genus has seen such a proportionate increase in numbers of species over this period, underscoring the cryptic nature of speciation in the genus *Miniopterus* (Goodman *et al.*, 2009*a*, 2009*b*). Genetic surveys have greatly aided the discovery of cryptic species in *Miniopterus*, especially among Afrotropical and Malagasy forms (Juste *et al.*, 2007; Goodman *et al.*, 2009*b*, 2011,

2015; Furman *et al.*, 2010; Puechmaille *et al.*, 2014; Monadjem *et al.*, 2019, 2020; Demos *et al.*, 2020). However, less attention has been paid to Asian forms, and for a long time, many larger *Miniopterus* from this continent were recognized as various subspecies of *M. schreibersii* (Simmons, 2005). This essentially Mediterranean species is now considered to be endemic to the Western Palaearctic and does not range east beyond the Caucasus (Šrámek *et al*., 2013).

In India and Sri Lanka, three distinctively sized species of *Miniopterus* are currently recognized: the small *M. pusillus* Dobson, 1876; medium-sized *M. fuliginosus* (Hodgson, 1835); and large *M. magnater* Sanborn, 1931 (Ibáñez and Juste, 2019; Saikia *et al.*, 2020). The Asian bent-winged bat, *M. fuliginosus* was described from central Nepal by B. H. Hodgson in 1835 and was long considered a subspecies of *M. schreibersii* (Kuhl, 1817). However, molecular phylogenetic studies (Appleton *et al.*, 2004; Tian *et al.*, 2004) established *M. fuliginosus* as a distinct species, confirming an earlier comprehensive morphological review (Maeda, 1982). *Miniopterus fuliginosus* is thought to range from northeastern Afghanistan and northern Pakistan, through India, Nepal, Sri Lanka, northern Myanmar, northern Vietnam, southern and eastern China, to Taiwan, Korean Peninsula, easternmost Russia, and Japan (Ibáñez and Juste, 2019). However, variation of *M. fuliginosus* across its range remains poorly studied, especially in South Asian countries. Populations in central and southern India and Sri Lanka appear geographically isolated from the rest of the species range. We sought to critically compare *Miniopterus* populations from southern India and Sri Lanka with typical *M. fuliginosus* in both molecular and morphological terms. Mitochondrial DNA sequences were used to assess the phylogenetic relationships of Indian and Sri Lankan *Miniopterus* species. Our findings show that *Miniopterus* populations in Peninsular India and Sri Lanka do not represent *M. fuliginosus* but differ from that species both genetically and morphologically. We describe it here as a species new to science.

Materials and Methods

Field Sampling

The Sri Lankan specimens newly reported in this study were collected during systematic surveys conducted from 2016 to 2020 in tea plantations and adjacent habitats of the wet zone of Sri Lanka. We surveyed 18 sites over an elevational range of 36–1673 m a.s.l. in Sri Lanka (Kusuminda *et al.*, 2018; Kusuminda *et al.*, 2020). Bats were captured in and around tea plantations and inside bat roosting sites using mist nets, harp trap, and hand nets. Three 2.5 × 12 m mist nets (mesh size 38 mm) were stacked vertically to create a 7.5 × 12 m capture area with the triple-high Forest Filter mist net system (Bat Conservation & Management, Carlisle, USA) to catch free flying bats. The triple-high mist net system was opened from sunset to midnight and monitored continuously. A G7 Forest Strainer Harp Trap with capture area of 1.8 × 2.4 m (Bat Conservation & Management, Carlisle, USA) was placed in front of selected day-roosting sites to capture bats during their evening emergence. The harp trap was left open in front of the day roosts until 7.00 pm and checked every 10 min. Hand nets were also extensively used to catch bats in most day roosts. Species were provisionally identified using external measurements following Bates and Harrison (1997). Bats of the genus *Miniopterus* were identified by the characteristic features of the genus, including an elongated second phalanx of the third digit, a rounded head, rounded ears, and a relatively long and slightly curved tragus. Diagnostic external morphometric measurements were taken using NEIKO digital calipers following Bates and Harrison (1997) and modified from Gaudin *et al*. (2016); these measurements are specified below under 'Morphometric Comparisons.' Tissue samples were taken by biopsy punch (3 mm) from the wing membrane of all live bats before releasing at their roosting sites. Wing biopsies were preserved in 95% ethanol. Eight individuals were preserved as voucher specimens and deposited at the National Museum of Sri Lanka, Colombo, Sri Lanka (NMSL) and National Wildlife Research and Training Centre, Giritale, Sri Lanka (NWRTC). Of the preserved specimens, only the holotype was genotyped. Bats were captured under permission of the Department of Wildlife Conservation of Sri Lanka (permit no.: WL/3/2/02/2016), and research procedures were approved by the ethical review committee of the Institute of Biology, Sri Lanka (ERC IOBSL165 11 17) and were in compliance with international field standards on use of wild mammals in research and education (Sikes *et al.*, 2016). Geographic coordinates and elevation of the study sites were recorded on a Garmin eTrex 20x GPS receiver.

DNA Extraction, Amplification and Sequencing

Whole genomic DNA was isolated from tissue samples of two individuals (one wing tissue and one muscle tissue) using a Wizard Genomic DNA Purification Kit (Promega Corporation, Madison, USA) following the manufacture's protocols. A 651 bp fragment of the cytochrome c oxidase subunit 1 (*COI*) gene was amplified via PCR using previously published primers VF1d 5'-TTCTCAACCAACCACAARGAYATYGG-3' and VR1d 5'-TAGACTTCTGGGTGGCCRAARAAYCA-3' (Ivanova *et al.*, 2007). The PCR was carried out in 25 µl reactions using ca. 20 ng of DNA templates, 0.5 µl of VF1d and VR1d primers (10 mM) respectively, 10.5 µl of nuclease free water, and 12.5 µl of Promega PCR master mix (2X). PCR conditions were as follows: initial denaturation of 1 min at 94°C, followed by five cycles of denaturation for 30 sec at 94°C, annealing for 40 sec at 50°C and extension for 1 min at 72°C followed by 35 cycles of denaturation for 30 sec at 94°C, annealing for 40 sec at 55°C and extension for 1 min at 72°C with a final extension for 10 min at 72°C (Lim *et al.*, 2016). The success of the PCR amplification and size of the amplified fragment was checked through gel electrophoresis in ethidium bromide-stained 1% Agarose gel using a Promega 100 bp ladder. Sequencing was

performed on an ABI 3730xl analyser (Applied Biosystems, CA, USA) with the PCR primers at the GeneTech, Sri Lanka. *COI* sequences generated in the present study are available from GenBank as accessions OL688877-OL688878.

Phylogenetic Analyses

Phylogenetic relationships of Sri Lankan and Indian populations of *Miniopterus* were evaluated using the mitochondrial *COI* gene. This gene is commonly used as a barcode marker for bats and represents the majority of DNA sequences available for *Miniopterus* species from Asia on GenBank and the Barcode of Life Database (BOLD).

Consensus sequences from forward and reverse reads were assembled in Geneious v5.6 (Drummond *et al.*, 2009). We downloaded all the available *COI* sequences for *Miniopterus* species known to occur in Asia (listed in Supplementary Appendix S1). Their species assignments follow recent publications (e.g., Francis *et al.*, 2010; Kruskop *et al.*, 2012; Li *et al.*, 2015; Ruedi *et al.*, 2021), which generated and utilized many of these sequences, allowing direct comparisons. Notice that one sequence from Panay, Philippines (MK410364 — Arai *et al.*, 2019) that was accessioned as *M. schreibersii* is referred here provisionally as *M.* cf. *eschscholtzii*, based on its geographic origin; this taxonomic assignment needs confirmation with properly identified specimens. *Chaerephon plicatus* (Buchannan, 1800) (Molossidae) was used as the outgroup (cf., Teeling *et al.*, 2016). The total dataset included 107 sequences comprising 10 of the 40 known *Miniopterus* species (Supplementary Appendix S1). DNA sequences were aligned using Geneious (Drummond *et al.*, 2009).

Mitochondrial *COI* gene trees were reconstructed using Bayesian and Maximum Likelihood methods. Partitioning schemes and best-fit substitution models for each partition were assessed using the Bayesian Information Criterion (BIC) implemented in Partitionfinder 2 (Lanfear *et al.*, 2017). BIC indicated three partitions based on the three codon positions with GTR + G substitution model for first and third codon positions and JC + G + I for the second codon position. Partitioned Maximum Likelihood analysis was implemented in RAxML v. 7.2.6. (Stamatakis *et al.*, 2008) with 200 independent Maximum Likelihood searches using the rapid hill climbing algorithm (Stamatakis *et al.*, 2007). Branch support was estimated using 1000 bootstrap pseudoreplicates. Partitioned Bayesian analysis was performed in MrBayes v. 3.2.6 (Ronquist and Huelsenbeck, 2003) with unlinked model parameters using default priors for 20 million generations with two independent runs and four chains (one hot and three cold chains) sampling every 10000 generations. Convergence of the independent runs was assessed by examining split frequencies (< 0.01) of clades across runs, effective sample sizes (ESS values) and likelihood plots in Tracer v. 1.4.1 (Rambaut *et al.*, 2018). An all-compatible consensus tree was built after the first 25% of sampled trees were discarded as burn-in. Uncorrected pairwise distances (p-distances) between species and groups were calculated in MEGA X with an average site cut-off of 95% (Kumar *et al.*, 2018).

Morphometric Comparison

Total of 75 specimens were examined to generate all data, 54 specimens were used to generate external measurements and 56 specimens were used to obtain craniodental measurements. The following standard external measurements were taken from 54 preserved specimens with digital calipers: total body length (HB), tail length (T), hindfoot length without claw (HF), tibia length (TIB), ear length (Ear), forearm length (FA), tragus length (Tr), third metacarpal length (d3m), fourth metacarpal length (d4m), fifth metacarpal length (d5m), first phalanx of third digit length (d3p1), and second phalanx of third digit length (d3p2). Total body length and tail length were taken to the closest 1.0 mm and all other external measurements were taken to the closest 0.1 mm. Body mass of live adult bats in cloth bags was taken with a Pesola spring balance to the closest 0.1 g.

A set of 15 craniodental measurements were taken with digital calipers to the closest 0.01 mm (modified from Monadjem *et al.*, 2020) from 56 adult specimens, identified by fully erupted adult dentition and the fusion of the basisphenoid-basioccipital suture. The cranial measurements were: GSKL, greatest skull length, from the anterior rim of the alveolus of the first upper incisor to the most projecting point of the occipital region; CIL, condyloincisive length, from exoccipital condyles to anterior rim of the alveolus of the first upper incisor; ZYW, zygomatic width, the greatest width of the skull across the zygomatic arches; POB, postorbital breadth, narrowest dorsal width posterior to the postorbital constriction of the cranium; MAW, mastoid width, the greatest width across the mastoid region; BCW, braincase width, greatest width of the braincase; LW, lachrymal width, greatest width across rostrum at lachrymal projections; and ML, mandible length, from the posterior-most point of the condyle to anterior-most alveoli of lower incisors. Dental measurements included: M3–M3, width across the upper third molars, taken across the outer-most point of the crowns of the 3rd upper molars; C–M3, complete upper canine-molar tooth row, taken from the anterior-most point of the crown of the upper canine to the posterior-most point of the crown of 3rd upper molar; I1–M3, complete upper tooth row, taken from the anterior-most point of the alveolus of the first upper incisor to the posterior-most point of the crown of 3rd upper molar; MOLS, complete upper molar tooth row, taken from the anterior-most point of the crown of the upper anterior premolar to the posterior-most point of the crown of 3rd upper molar; C–C, width across upper canines, taken across the outer-most points of the crowns of the upper canines; mols, complete mandibular molar tooth row, taken from the anterior-most point of the crown of the lower anterior premolar to the posterior-most point of the crown of 3rd lower molar; and i1–m3, complete mandibular tooth row, taken from the anterior-most point of the alveolus of the first lower incisor to the posterior-most point of the crown of 3rd lower molar. Tooth abbreviations are as follows: I = incisor, C = canine, P = premolar, M = molar; with upper teeth presented in upper case and lower teeth in lower case. A principal components analysis (PCA) of log-transformed values of these cranial and dental measurements was conducted on the variance-covariance matrix in the program PAST (Hammer *et al.*, 2001) to compare the morphology of the various taxa. To determine which craniodental variables were most useful to separate *M. fuliginosus* from the new species, we used Linear discriminant analysis (LDA) in the program PAST (Hammer *et al.*, 2001) based on the 15 log-transformed craniodental variables. A priori classification based on species designations from the molecular genetic analysis and morphological comparisons was used. General classifier and Jackknife estimator in LDA were calculated using program PAST to cross validate prior classification. In addition, differences between *M. fuliginosus* and the

new species were assessed using Minitab 17: two sample *t*-tests evaluated differences in 15 craniodental measurements, whereas Mann-Whitney *U*-tests were performed on ratio between TIB and FA, d3p2 and d3m. A *P*-value less than 0.05 was taken to reflect a significant difference.

This study is based on 75 specimens deposited in the following museums: National Museum of Sri Lanka, Colombo, Sri Lanka (NMSL); National Wildlife Research and Training Centre, Giritale, Sri Lanka (NWRTC); Harrison Institute (formerly Harrison Zoological Museum), Sevenoaks, UK (HZM); Zoological Museum of Moscow University, Russia (ZMMU); Hungarian Natural History Museum, Budapest, Hungary (HNHM), Muséum d'histoire naturelle de Genève, Geneva, Switzerland (MHNG) and Zoological Survey of India, Regional Centres at Shillong and Solan, India (ZSI) (Supplementary Appendix S2).

Acoustic Analysis

Echolocation calls were recorded from three bats captured at the type locality and subsequently released. Recordings were taken from individuals flying in a closed room (5 × 3.5 × 2.5 m) using a Pettersson M500 microphone (Pettersson Elektronik, Uppsala, Sweden) connected to Lenovo Mini 10 ThinkPad at a sampling frequency of 500 kHz. Calls were analyzed using Kaleidoscope v4.3.2 (Wildlife Acoustics, Maynard, USA) to measure peak frequency in a Hanning window with FFT size of 1024.

Results

Phylogenetic Relationships

Both Bayesian analyses (Fig. 1) and Maximum Likelihood (Supplementary Fig. S1) recovered highly similar topologies and branch lengths. Sequences of *Miniopterus* from Sri Lanka and South India were recovered in a strongly supported (bootstrap support ≥ 80, posterior probability ≥ 0.95) clade distinct from other South Asian *Miniopterus*; this newly described clade was sister to a well-supported clade comprising *Miniopterus* cf. *eschscholtzii* from the Philippines and the sister taxa *M. fuliginosus* and *M. magnater* (Fig. 1). Together, these two clades, comprising medium and large *Miniopterus*, was then sister to a clade containing the small *M. pusillus* and other Asian species. The mean uncorrected pairwise sequence divergence among three sequences of the newly described *Miniopterus* lineage was 0.83% (range 0.4–1.2%). The pairwise sequence divergence between these sequences and other sampled taxa averaged 12.7% (range 8.5–15.9%) (Table 1); the lowest (8.5%) divergence was with *M.* cf. *eschscholtzii* from the Philippines while the highest (15.9%) was with *M. schreibersii* from Europe (Greece, Italy, Spain).

Morphometric Analyses

The first axis of the PCA accounted for 88.8% of the total variance (Table 2). All variable loadings on this axis (PC1) were highly correlated and positive, indicating a general size vector, so that the largest species (*M. magnater*) is on the right of the ordination and the smallest (*M. pusillus*) is on the left. Variables had both high and low loadings on the second principal component (PC2), which accounted for 3.3% of overall variation and reflects shape differences. The largest positive loading was with C–C (0.465) and the largest negative loading was with LW (-0.746) suggesting that skull width is reflected in dispersion of samples on this component (Table 2). *M. fuliginosus* from Eastern and Southeastern Asia and representatives of the new lineage from Sri Lanka and South India fall into separate clusters with slight overlap (Fig. 2).

Linear discriminant analysis confirms the distinction of the new lineage from Sri Lanka and southern India from *M. fuliginosus*. Four craniodental variables contributed importantly to their discrimination; loadings of these variables on the first axis of LDA are LW (0.0075), MAW (0.0037), GSKL (0.0034) and M3–M3 (0.0032). All except one individual (n=13) of *M. fuliginosus* were correctly identified (93%) and all individuals (n = 22) of the new lineage of *Miniopterus* from Sri Lanka and South India were correctly identified (100%). Overall percentages of general classifier and Jackknife estimator for correct classification are 97.2% and 75% respectively (Supplementary Appendix S3). On the basis of its distinction in the molecular phylogeny and its clear separation from other species of *Miniopterus* in the craniodental analyses, we believe that there is substantial evidence to consider that these Sri Lankan and South Indian specimens belong to a hitherto undescribed species. Hence, we describe it here as a new species.

Description of the new species

Family Miniopteridae Dobson, 1875

Genus *Miniopterus* Bonaparte, 1837

Miniopterus phillipsi sp. nov.

Phillips's Long fingered Bat

Synonymy

Miniopterus schreibersii Blanford, 1891 (in part): not *Vespertilio schreibersii* Kuhl, 1817.

Miniopterus fuliginosus Tian *et al*., 2004 (in part): not *Vespertilio fuliginosus* Hodgson, 1835.

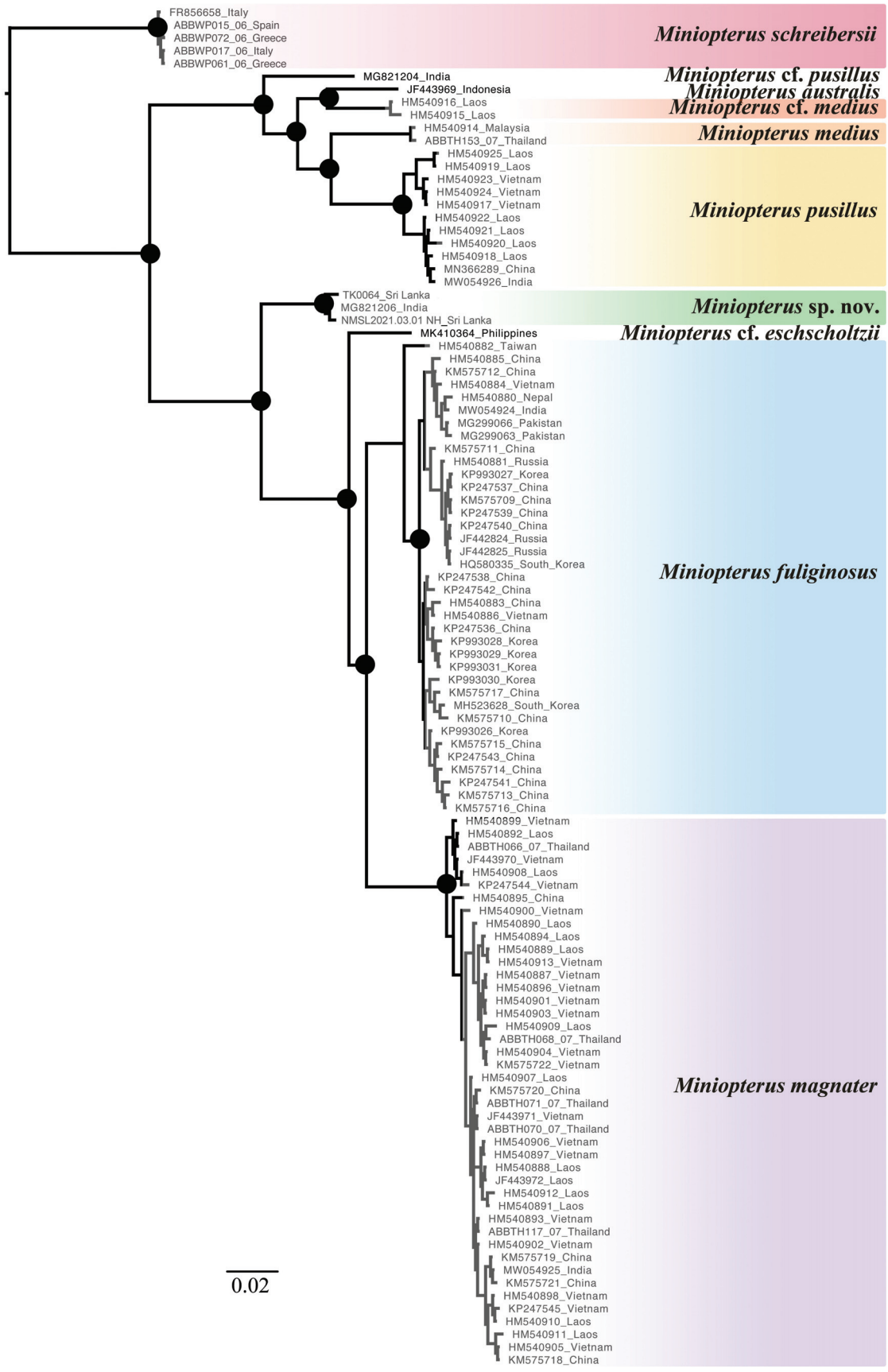

FIG. 1. Bayesian majority-rule consensus tree of the *COI* gene of Asian *Miniopterus* species. Dark circles depict nodes with Bayesian posterior probability ≥ 0.95 and maximum likelihood bootstrap support ≥ 70. The outgroup *Chaerephon plicatus* is not shown. Scale bar indicates the number of substitutions per site

TABLE 1. Uncorrected pairwise genetic distances in the *COI* gene between analyzed species of *Miniopterus*. Distances involving the new species are boldfaced

Species	2	3	4	5	6	7	8	9	10
1. *M. magnater*	7.28	16.25	13.62	14.10	16.35	15.87	6.71	**8.95**	15.46
2. *M.* cf. *eschscholtzii*	–	15.86	13.44	12.80	15.20	14.97	5.12	**8.46**	13.88
3. *M. schreibersii*		–	15.20	15.38	16.52	16.96	15.80	**15.92**	14.32
4. *M.* cf. *pusillus*			–	10.03	8.37	10.20	13.68	**14.27**	8.81
5. *M. pusillus*				–	8.49	8.57	12.92	**14.33**	8.05
6. *M.* cf. *medius*					–	9.09	15.49	**15.58**	4.85
7. *M. medius*						–	14.99	**14.74**	8.87
8. *M. fuliginosus*							–	**9.27**	14.10
9. *M. phillipsi* sp. nov.								–	14.05
10. *M. australis*									–

Holotype

NMSL 2021.03.01.NH (field no. TK0122), collected by Tharaka Kusuminda and Mathisha Karunarathne on 29 January 2019. An adult female preserved in 70% alcohol and deposited at National Museum of Sri Lanka, the skull has been extracted and cleaned. There is a scar on left shoulder of the specimen made while collecting the tissue sample. Its partial *COI* sequence is available from GenBank as accession OL688878.

Type locality

Idulgashinna cave, near Idulgashinna railway station (6.779131 N, 80.896704 E; 1590 m a.s.l. — Fig. 3 and Supplementary Fig. S2), at an edge of Dunkanda division of Bio Tea Garden tea plantation in the Badulla District, Uva Province, Sri Lanka. The holotype was collected in a harp trap set in front of the cave entrance.

Paratypes

Two adult male specimens NMSL 2021.03.02.NH and NMSL 2021.03.03.NH, collected at the same locality as the holotype on 29 January 2019 (Fig. 4). These two specimens are currently preserved in 70% alcohol at National Museum of Sri Lanka. Tongue muscle of NMSL 2021.03.02.NH was preserved in 99% ethanol. The skulls were extracted and cleaned. The paratypes were not sequenced.

Referred specimens

Two specimens (NMSL 177C and NWRTC TK156) were collected from mid-elevations in Kegalle District of Central Sri Lanka (a cave in Sandaraja forest, Doteloya, Aranayaka, Sri Lanka on 02 January 2019). These two specimens have not been sequenced for *COI* gene, but one (NMSL 177C) has been sequenced for the mitochondrial 16S gene and was determined to be the same species (T. Kusuminda, A. Mannakkara, K. D. B. Ukuwela, M. Karunarathna, B. D. Patterson, and W. B. Yapa, In litt.). Moreover, these two specimens are morphologically identifiable as *M. phillipsi* sp. nov. by LDA. A biopsy punch was obtained from a *Miniopterus* captured and released (field no. TK0064) near the Tea Research Institute in Nuwara Eliya District (Talawakele, Sri Lanka on 02 October 2018). This individual's *COI* sequence (GenBank no. OL688877) was 98% similar to the holotype's sequence, hence it was identified as *M. phillipsi* sp. nov. Another three specimens (NMSL 177D, NWRTC TK117 and HZM 263.29194) were collected from Wavulgalge cave, Nikapitiya, Wellwaya (Moneragala District of Sri Lanka) and four specimens (NMSL 177E, HZM 260.27644, HZM 261.27645 and HZM 262.29137) were collected from Wavulpane cave, Pallebedda (Ratnapura District of Sri Lanka). These seven specimens have not been sequenced but morphological similarities and LDA assignments provisionally assign them to

TABLE 2. Eigenvector loadings for the first two components of the principal component analysis of log-transformed cranial and dental measurements of *M. phillipsi* sp. nov., *M. fuliginosus*, *M. magnater* and *M. pusillus*

Character	PC1	PC2
GSKL	0.217	-0.040
CIL	0.233	0.099
ZYW	0.236	0.130
POB	0.168	0.154
MAW	0.173	-0.105
BCW	0.135	0.103
LW	0.357	-0.750
ML	0.288	0.122
C–C	0.294	0.466
M3–M3	0.308	0.073
C–M3	0.289	0.120
I1–M3	0.284	-0.022
i1–m3	0.262	-0.137
MOLS	0.283	0.230
mols	0.250	-0.211
Cumulative total variation explained (%)	88.8	92.1

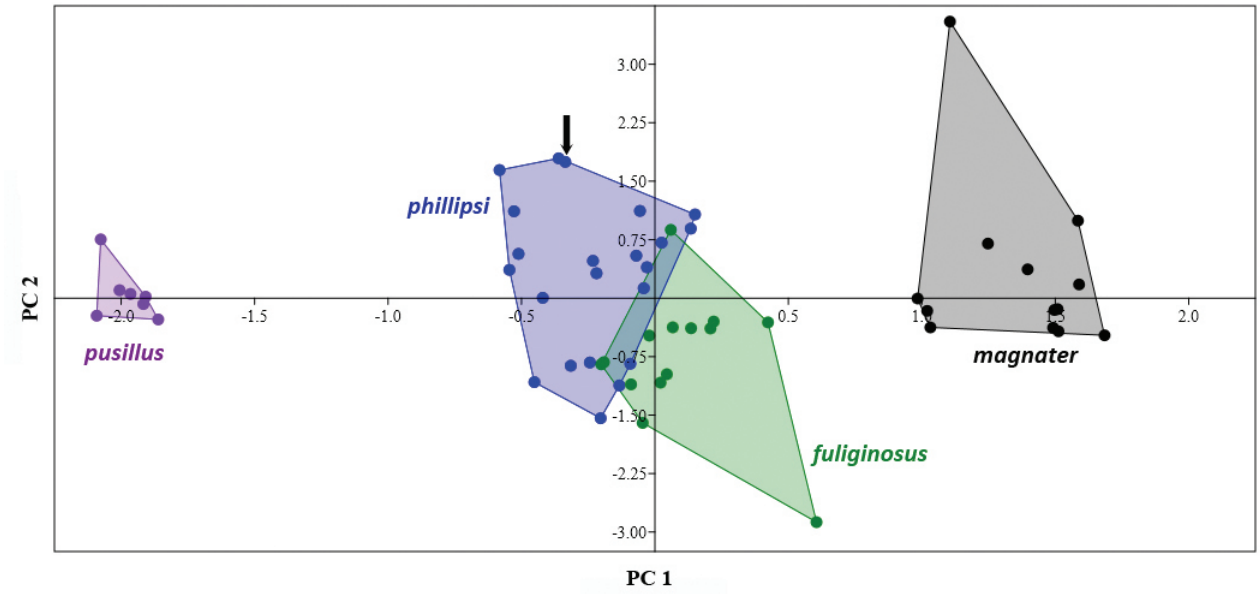

FIG. 2. Plot of the first two components of a principal component (PC) analysis for craniodental measurements of the *Miniopterus* species in India and Sri Lanka (*M. philipsii* sp. nov. — blue circle; *M. fuliginosus* — green circle; *M. magnater* — black circle; *M. pusillus* — purple circle). Arrow points to holotype. See Table 2 for the variables used in this analysis and the loadings on PC1 and PC2

M. phillipsi sp. nov. Likewise, 18 specimens collected from Western India (HZM 258.25669, HZM 254.25009, HNHM 92.156.1–HNHM 92.124.16) have not been sequenced but were identified morphologically as *M. phillipsi* sp. nov. using LDA; they were obtained from the same colony where a genotyped individual for *COI* gene (GenBank no. MG821206 — C. Srinivasulu, B. Srinivasulu, T. A.

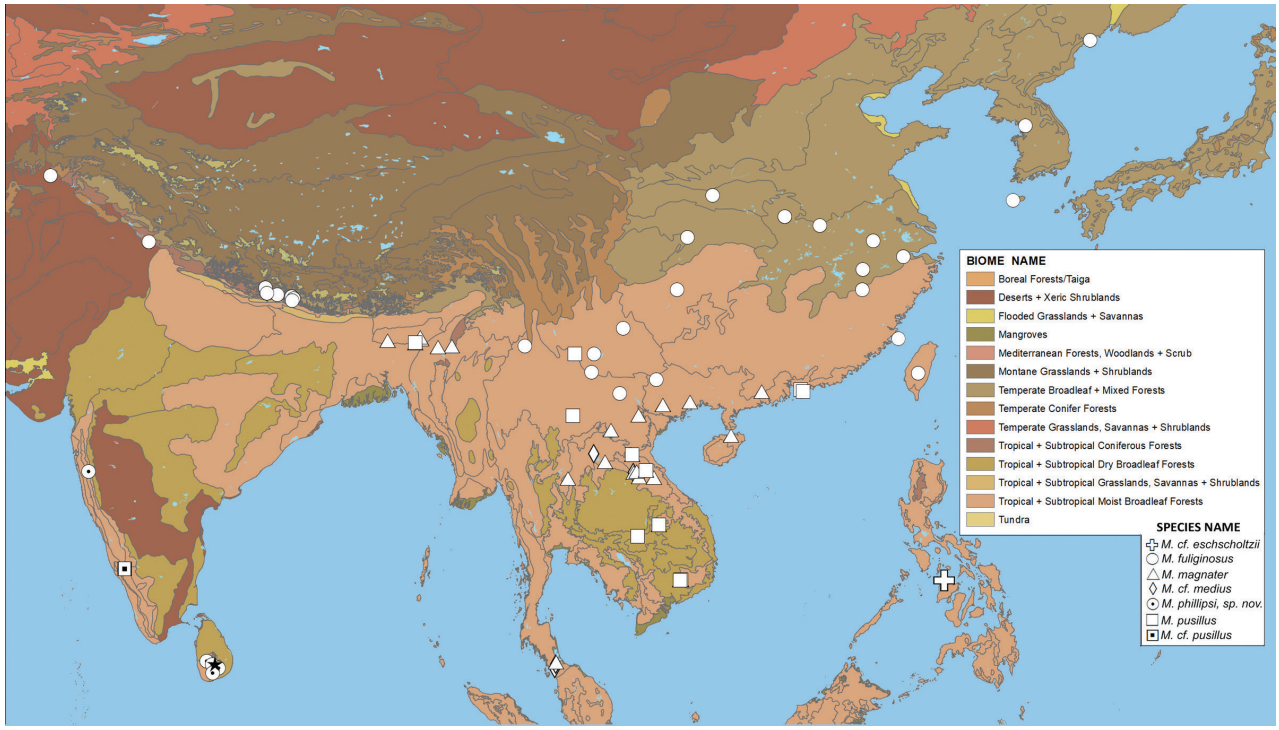

FIG. 3. Map of South and Southeast Asia showing sampling localities of *M. phillipsi* sp. nov. and *Miniopterus* specimens of mainland Asia mentioned in this study with biomes of ecoregions (Dinerstein *et al*., 2017). Type locality of *M. phillipsi* sp. nov. is marked by a black star

FIG. 4. Portrait of *M. phillipsi* sp. nov. NMSL 2021.03.02.NH

Shah, and G. Devender, unpublished data) was collected, i.e. Robbers' Cave, near Mahabaleswar, Maharashtra, India (Fig. 3).

Etymology

This species is named after W. W. A. Phillips (William Watt Addison Phillips, 1892–1981) in recognition of his immense contributions to studies on the mammals of Sri Lanka and South Asia. Phillips was born and grew up in England and he was a nature lover since his childhood. He was a tea planter by profession and came to Ceylon (now Sri Lanka) in 1911.

Diagnosis

Miniopterus phillipsi sp. nov. is distinguished by its intermediate size from both smaller and larger congeners in India and Sri Lanka. *M. pusillus* is much smaller than *M. phillipsi* sp. nov. in the external measurements TIB (< 18 mm), FA (< 43 mm), d3m (< 40 mm), d4m (< 38 mm) and d5m (< 36 mm) and in skull length (GSKL < 14.7 mm). *M. phillipsi* sp. nov. is distinguished from *M. magnater* by the latter's larger external measurements (HB > 56 mm and d3m > 46 mm) and skull size (GLSK > 16.4 mm — Tables 3 and 4). The new species is generally smaller than *M. fuliginosus* in both external and cranial dimensions, although there is slight overlap (Figs. 5–7). There are significant differences between *M. phillipsi* sp. nov. and *M. fuliginosus* in GSKL ($P < 0.001$), ZYW ($P = 0.026$), MAW ($P < 0.001$), BCW ($P = 0.046$), LW ($P = 0.001$), ML ($P = 0.001$), M3–M3 ($P = 0.002$), C–M3 ($P = 0.002$), I1–M3 ($P = 0.001$) and i1–m3 ($P < 0.001$). In all of these craniodental characters, *M. fuliginosus* is larger than *M. phillipsi* sp. nov. (Tables 4 and 5). *Miniopterus phillipsi* sp. nov. also differs significantly from *M. fuliginosus* in the ratio of tibia to forearm length (TIB/FA; $P = 0.002$) and the ratio of second phalanx of third digit to third metacarpal (d3mp2/d3m; $P = 0.023$). In *M. phillipsi* sp. nov., TIB/FA ratio is usually higher (median: 42.16%, range: 41.1–43.9%) than in *M. fuliginosus* (40.78%, 39.6–42.1%), whereas d3mp2/d3m ratio is lower (83.27%, 79.3–90.4% versus 88.55%, 81.6–90.9%, respectively). The tragus of *M. phillipsi* sp. nov. is medium-sized in both length and width.

TABLE 3. External measurements (mm) and mass (g) of *M. phillipsi* sp. nov. from Idulgashinna, Sri Lanka. Measurements presented as $\bar{x} \pm$ SD, range, and sample size *n*. Measurements of the holotype, paratypes and other individuals of the new species and other species of *Miniopterus* occurring in India and Sri Lanka are shown for comparative purposes. Measurements of *M. phillipsi* sp. nov. types were taken by TK, while the other specimens by an assortment of different authors

Specimen or taxon	HB	T	HF	TIB	FA	Ear
M. phillipsi sp. nov. Holotype ♀ NMSL 2021.03.01.NH	50	55	9.49	19.62	46.71	12.12
M. phillipsi sp. nov. Paratype ♂ NMSL 2021.03.02.NH	56	56	9.53	20.65	47.52	11.10
M. phillipsi sp. nov. Paratype ♂ NMSL 2021.03.03.NH	54	54	8.77	20.05	46.64	11.82
M. phillipsi sp. nov., all specimens	52.0 ± 1.70 50–56, *19*	53.2 ± 3.25 48–58, *18*	9.3 ± 0.54 8–10, *19*	19.7 ± 0.45 19–20, *19*	46.7 ± 1.05 44–49, *19*	12.0 ± 0.65 11.1–12.8, *8*
M. fuliginosus	55.2 ± 4.74 47–63, *10*	54.2 ± 5.35 46–60, *8*	9.2 ± 0.98 7–10, *10*	19.2 ± 1.21 17–20, *9*	46.9 ± 2.39 42–49, *10*	12.3 ± 0.57 11.7–12.9, *4*
M. magnater	61.0 ± 2.44 56–65, *14*	59.0 ± 2.00 56–64, *15*	9.8 ± 0.56 9–10, *16*	21.2 ± 0.84 20–22, *16*	50.5 ± 1.21 48–52, *16*	12.4 ± 1.18 10.5–14.4, *16*
M. pusillus	48.2 ± 4.64 42–57, *9*	47.9 ± 2.63 43–51, *7*	8.1 ± 0.55 7–8, *9*	17.1 ± 0.78 15–17, *9*	41.7 ± 0.90 39–42, *9*	10.4 ± 0.43 10–11, *4*

The tragus of *M. magnater* is longer, broader, and more pointed towards the tip than the other three species in India and Sri Lanka. The middle of the tragus is much broader than its base and tip in *M. magnater* (slightly broader in *M. phillipsi* sp. nov.). The tragus of *M. fuliginosus* has parallel margins along most of its length, as does that of *M. pusillus.* However, the tragus of *M. pusillus* is shorter in length and barely curved forward compared to the other three species (Fig. 8).

Description

Miniopterus phillipsi sp. nov. is a medium-sized bat (FA 44–49 mm) exhibiting the typical features of the genus i.e. an elongated second phalanx of the third digit, short and rounded ears, high forehead, short and broad muzzle, and slender and slightly curved tragus with rounded tip (Supplementary Fig. S3). Tail length approximately equals head-and-body length (Table 3). The ear is relatively short and rounded (ca. 12 mm in length) and not readily distinguishable from that of *M. fuliginosus* (Table 3). The tragus is medium sized (5 mm) and slightly curved forward with a rounded tip (Fig. 8). The external measurements of the holotype, paratypes and other specimens of *M. phillipsi* sp. nov. are given in Table 3. Fur is dense and soft, fairly long above and short below. Fur slightly extending onto the membranes ventrally, but dorsally confined to the body. The pelage is chocolate-brown above and slightly paler on the under parts (Supplementary Fig. S4). Individual hairs are the same color throughout. The skull of *M. phillipsi* sp. nov. has a wide rostrum and round braincase typical of the genus (Figs. 5–7). Cranial measurements for the holotype and paratypes of *M. phillipsi* sp. nov. are shown in Table 4. The dentition of *M. phillipsi* sp. nov. is I 2/3, C 1/1, P 2/3, M 3/3, which is typical of the genus *Miniopterus*. Dental measurements of the holotype and paratypes of *M. phillipsi* sp. nov. are shown in Table 5.

Natural History

This species is distributed from lower to higher elevations (263–1590 m) of wet and intermediate climatic zones of Sri Lanka. The type locality is the highest elevation it was captured (1590 m); specimens captured at Talawakele (1411 m) document its range in the central highlands of Sri Lanka. Specimens captured at Doteloya were roosting in a granite cave at the edge of a tropical wet lowland rainforest (Survey Department of Sri Lanka, 2012). Wellawaya and Pallebedda records lie at lower elevations of intermediate climatic zone of Sri Lanka. In western India, it was recorded from Robbers' Cave, located in the evergreen forest of Mahabaleshwar region of northern Western Ghats at an elevation of 1217 m.

Like other members of this genus, this species apparently prefers to roost in caves and tunnels. Colony sizes of this species are estimated at 1,300–1,500 bats in Idulgashinna Cave, 700–1000 bats in Wavulgalge Cave, Wellawaya (Yapa *et al.*, 2005), 50–100 bats in Sandaraja Cave, Doteloya (Kusuminda *et al.*, 2020), 200,000 bats in Wavulpane Cave, Pallebedda (Digana, 2004), and 4,200 bats in Robbers' Cave, Mahabaleshwar (Korad *et al.*, 2006). Pregnant and lactating females of this species were reported in July and August

TABLE 3. Extended

Specimen or taxon	Tr	d3m	d4m	d5m	d3mp1	d3mp2	Body mass
M. phillipsi sp. nov. Holotype ♀ NMSL 2021.03.01.NH	5.54	43.85	41.60	37.87	11.95	37.12	10.5
M. phillipsi sp. nov. Paratype ♂ NMSL 2021.03.02.NH	5.21	45.59	42.47	38.80	11.76	37.32	10.5
M. phillipsi sp. nov. Paratype ♂ NMSL 2021.03.03.NH	5.45	44.48	41.61	37.87	11.60	35.39	10.0
M. phillipsi sp. nov., all specimens	5.4 ± 0.19 5.2–5.7, *8*	43.9 ± 1.07 42–45, *19*	41.9 ± 1.08 39–43, *19*	38.2 ± 0.92 36–39, *19*	10.7 ± 0.76 9–11, *19*	37.0 ± 1.59 34–40, *19*	
M. fuliginosus	5.6 ± 0.24 5.5–5.9, *3*	42.7 ± 2.38 38–45, *9*	41.0 ± 2.41 36–43, *9*	37.9 ± 1.82 34–39, *9*	10.3 ± 1.01 9–11, *9*	37.3 ± 2.78 32–40, *9*	
M. magnater	5.9 ± 0.57 4.9–7.1, *16*	47.1 ± 0.47 46–48, *8*	44.6 ± 0.68 43–45, *8*	40.1 ± 0.39 39–40, *8*	11.9 ± 0.26 11–12, *8*	41.1 ± 0.89 40–42, *8*	
M. pusillus	5.2 ± 0.35 4–5, *4*	38.1 ± 0.81 37–39, *6*	36.7 ± 1.08 34–37, *6*	34.5 ± 0.97 32–35, *6*	9.5 ± 0.65 8–10, *6*	32.9 ± 1.75 31–35, *6*	

TABLE 4. Cranial measurements (mm) of *M. phillipsi* sp. nov. from Idulgashinna, Sri Lanka. Measurements presented as $\bar{x} \pm$ SD, range, and sample size *n*. Measurements of the holotype, paratypes and other individuals of the new species and other species of *Miniopterus* occurring in India and Sri Lanka are shown for comparative purposes. Measurements of *M. phillipsi* sp. nov. types were taken by TK, while the other specimens by an assortment of different authors

Specimen or taxon	GSKL	CIL	ZYW	POB	MAW	BCW	LW	ML
M. phillipsi sp. nov. Holotype ♀, NMSL 2021.03.01.NH	15.23	14.72	8.87	3.97	8.47	8.07	4.77	11.19
M. phillipsi sp. nov. Paratype ♂, NMSL 2021.03.02.NH	15.08	14.82	8.65	3.85	8.66	7.84	4.70	11.05
M. phillipsi sp. nov. Paratype ♂, NMSL 2021.03.03.NH	15.67	15.18	8.77	3.95	8.77	8.23	4.97	11.28
M. phillipsi sp. nov., all specimens	15.4 ± 0.24	14.9 ± 0.26	8.7 ± 0.12	3.9 ± 0.08	8.6 ± 0.13	8.0 ± 0.13	5.1 ± 0.23	11.2 ± 0.18
	14.9–15.8, *22*	14.5–15.6, *22*	8.5–9.0, *21*	3.8–4.1, *22*	8.4–8.9, *21*	7.8–8.2, *22*	4.6–5.4, *22*	10.8–11.6, *22*
M. fuliginosus	15.8 ± 0.26	15.1 ± 0.30	8.8 ± 0.15	3.9 ± 0.05	8.8 ± 0.12	8.1 ± 0.10	5.4 ± 0.24	11.4 ± 0.20
	15.3–16.4, *14*	14.8–15.7, *14*	8.6–9.1, *13*	3.9–4.1, *14*	8.6–9.0, *14*	7.9–8.2, *14*	5.0–6.1, *14*	11.1–11.9, *14*
M. magnater	16.7 ± 0.19	16.3 ± 0.27	9.5 ± 0.28	4.1 ± 0.11	9.2 ± 0.24	8.5 ± 0.20	5.9 ± 0.26	12.4 ± 0.35
	16.4–17.0, *13*	15.9–16.7, *13*	9.1–10.0, *13*	4.0–4.3, *13*	8.8–9.5, *12*	8.2–8.7, *13*	5.5–6.3, *12*	12.0–13.0, *13*
M. pusillus	14.1 ± 0.22	13.6 ± 0.17	7.8 ± 0.09	3.6 ± 0.08	8.0 ± 0.08	7.6 ± 0.19	4.4 ± 0.09	9.9 ± 0.12
	13.8–14.5, *7*	13.4–13.8, *7*	7.7–7.9, *7*	3.5–3.7, *7*	7.9–8.1, *7*	7.3–7.9, *7*	4.3–4.5, *7*	9.7–10.0, *7*

in Sri Lanka (Digana, 2004; Kusuminda *et al.*, 2018).

Echolocation calls of recorded *M. phillipsi* sp. nov. had a mean peak frequency (± SD) of 52.8 kHz ± 0.72 kHz (range: 51–54 kHz, $n = 15$), which did not differ from those reported for *M. fuliginosus* from Western Himalaya, India (53.1 kHz in Chakravarty *et al*., 2020) or from eight colonies in China (53–58 kHz in Zhang *et al*., 2018). Other *Miniopterus* originally reported as *fuliginosus* but presumably pertaining to *M. phillipsi* sp. nov. include bats from the Western Ghats, India (52.0 kHz in Wordley *et al*., 2014) and from Kerala, India (53.2 kHz in Srinivasulu and Srinivasulu, 2017). It appears that the new species is not distinguished from *M. fuliginosus* in echolocation calls.

DISCUSSION

Our morphological and molecular analyses of South Asian *Miniopterus* uncovered the presence of a yet undescribed cryptic species in southern India and Sri Lanka. Phylogenetic analyses of mitochondrial *COI* sequences of Asian *Miniopterus* provide clear indications that *M. phillipsi* sp. nov. is a distinct species. Both Bayesian and Maximum Likelihood analyses recover both the new species and *M. fuliginosus* in reciprocally monophyletic groupings; in fact, on the basis of *COI* sequences, the two are not even sister taxa. Analyses securely recovered the clade of *M. fuliginosus* and *M. magnater*, and this clade was closely related to a distinctive lineage from the Philippines accessioned in GenBank as '*M. schreibersii*' (MK410364), but likely representing the endemic *M. eschscholtzii*. *Miniopterus phillipsi* sp. nov. is strongly supported as sister to the clade of these three species (Fig. 1). Mitochondrial markers have been widely used in other studies on *Miniopterus* spp. (Goodman *et al*., 2008, 2009*a*, 2010, 2015; Puechmaille *et al*., 2014; Monadjem *et al*., 2019, 2020). The new species has been described based on substantial mitochondrial DNA divergence (8.46–9.27%) from close relatives. The level of mitochondrial DNA divergence equals or exceeds those in other published studies on *Miniopterus* species (Goodman *et al*., 2008, 2009*a*, 2010; Puechmaille *et al*., 2014). For instance, these genetic distances considerably exceed mitochondrial DNA divergence between *M. wilsoni* and *M. minor* (4.1–5.7%) in Monadjem *et al*. (2020) or the 3.3% divergence between *M. ambohitrensis* and *M. aelleni* in Goodman *et al*. (2015). Strikingly, the various Malagasy species of *Miniopterus* studied by

Goodman and collaborators were reexamined using five nuclear intron sequences, and in each case their distinction as valid species was maintained (Demos *et al*., 2020). Likewise, the two cryptic species *M. schreibersii* and *M. maghrebensis* differed minimally at mitochondrial genes (1.2%), yet according to nuclear markers showed no evidence of interbreeding in areas of sympatry (Puechmaille *et al*., 2014).

Additional evidence of the distinction of the new species is provided by the *COI* sequences of *M. fuliginosus*, which were all clustered together in the same clade with minimal divergence. The large geographic range of this species includes Pakistan, northern India, Nepal, Vietnam, China, south-eastern extreme of Russia and Japan; it does not include southern India or Sri Lanka. In such a vast area, the genetic differences between *M. fuliginosus* individuals are less than between *M. fuliginosus* and *M. phillipsi* sp. nov. Still, because discordance between nuclear and mitochondrial sequences is common in other groups of bats (e.g., Furman *et al*., 2014; Dool *et al*., 2016; Mao and Rossiter, 2020), nuclear sequences will be needed to confirm the systematic relationships among these Asian *Miniopterus*.

The inclusion of additional sequences based on carefully identified and vouchered specimens are also needed to further clarify pending problematic relationships evident in our tree (Fig. 1). Indeed, one sequence from India labeled as '*M. pusillus*' (MG821204 — C. Srinivasulu, B. Srinivasulu, T. A. Shah, and G. Devender, unpublished data) appears to belong to a distinct species, with a sequence divergence of 10.0% from properly identified *M. pusillus* from northern India (Ruedi *et al.*, 2021). Three other samples from Laos and Malaysia were identified as *M. medius* by Francis *et al.* (2010) but appeared in distinct clades, with 9.1% sequence divergence between these groups. The Philippine sequence reported as '*M. schreibersii*' also deserves renewed inspection, as previously mentioned. More systematic work on Asian *Miniopterus* is needed to document and fully decipher species diversity in this difficult taxonomic group. Clearly, the names associated with *Miniopterus* records in public repositories — whether GenBank, BOLD or GBIF — should be critically reevaluated before being used in any publication.

In terms of morphology, our samples of *M. magnater* and *M. fuliginosus* exhibit overlap in measurements of ZYW, POB, MAW, BCW, LW, C–C, i1–m3 and mols. However, all studies agree that despite slight overlap for some measurements, Indian *M. pusillus*, *M. fuliginosus*, and *M. magnater* are all morphologically and genetically distinct species (Saikia *et al*., 2020; Ruedi *et al*., 2021). For

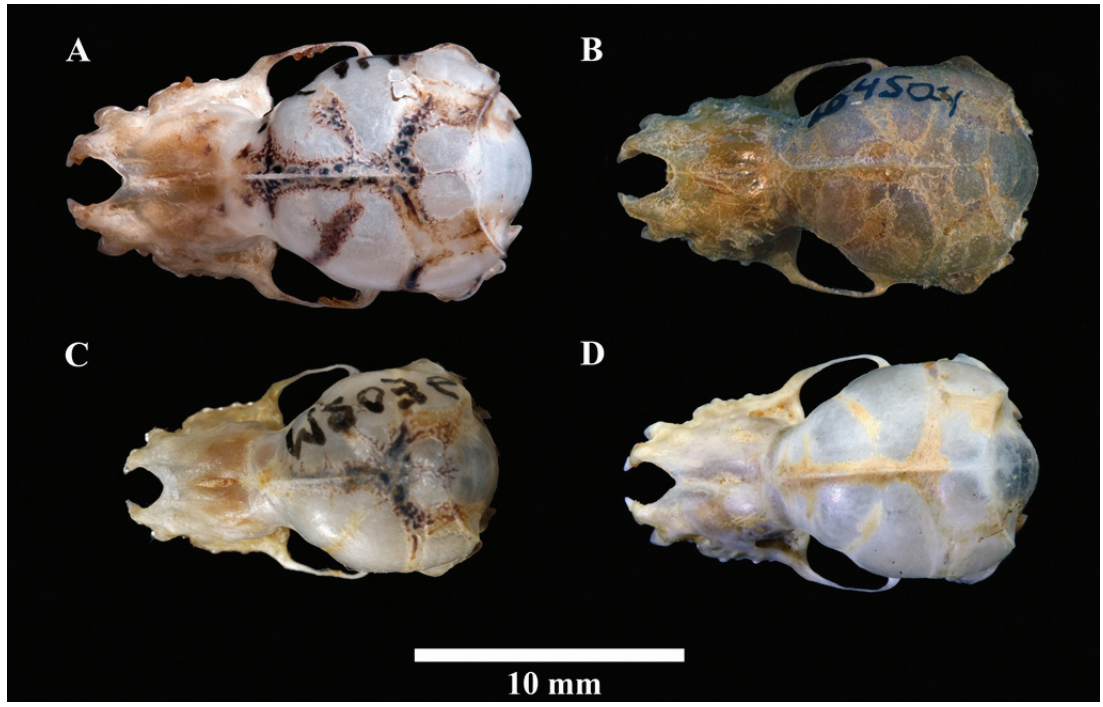

FIG. 5. Dorsal aspect of cranium of *Miniopterus* species in India and Sri Lanka. A — *M. magnater* (MHNG 1981.071); B — *M. fuliginosus* (ZMMU S-164504); C — *M. pusillus* (V/M/ERS/570); D — *M. phillipsi* sp. nov. (NMSL 2021.03.01.NH, holotype)

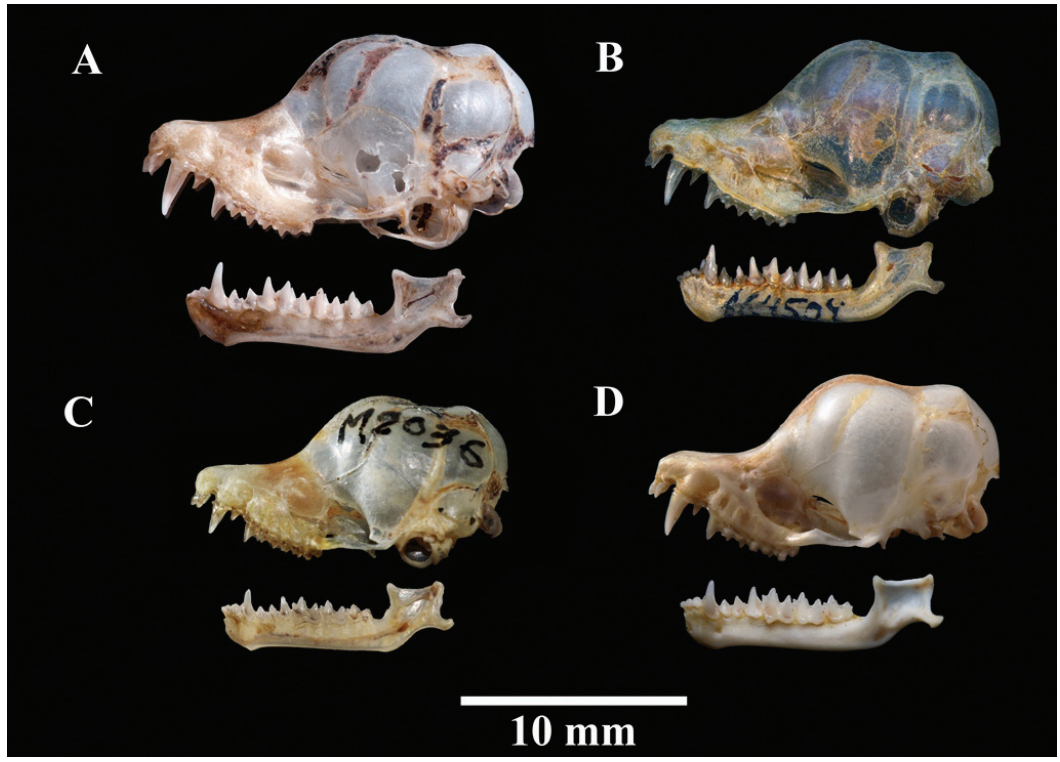

FIG. 6. Lateral aspect of cranium and mandible of *Miniopterus* species in India and Sri Lanka. A — *M. magnater* (MHNG 1981.071); B — *M. fuliginosus* (ZMMU S-164504); C — *M. pusillus* (V/M/ERS/570); D — *M. phillipsi* sp. nov. (NMSL 2021.03.01.NH, holotype)

the southern part of the Indian Subcontinent, we show here the clear distinction of the two morphologically most similar pairs, *M. fuliginosus* and *M. phillipsi* sp. nov. (Figs. 1 and 2). This corroborates the idea that South Asian species of *Miniopterus* differ morphologically chiefly in size

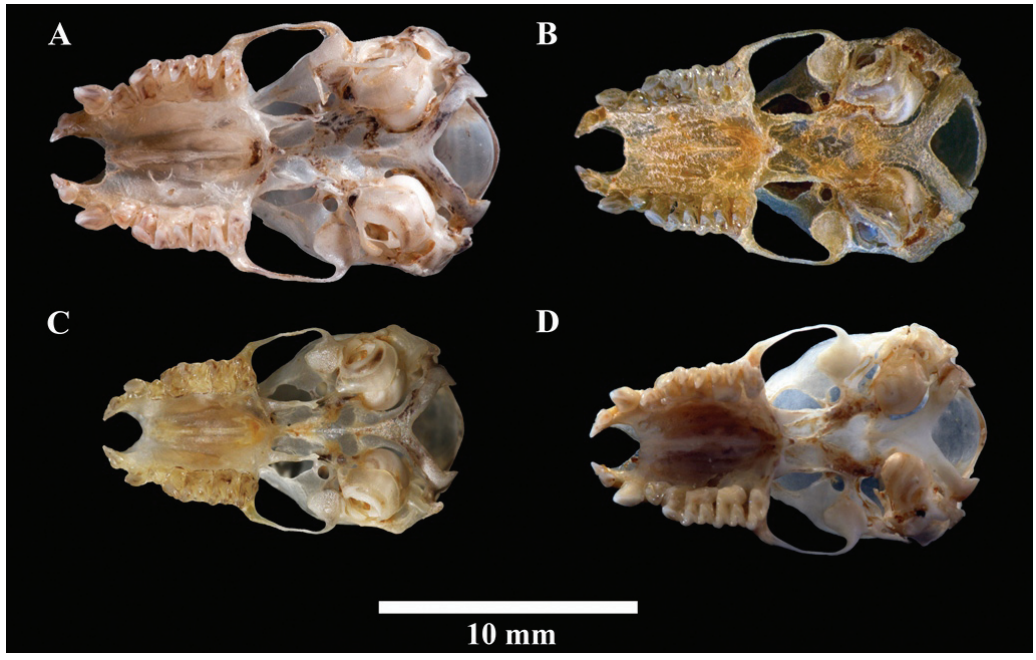

FIG. 7. Ventral aspect of cranium of *Miniopterus* species in India and Sri Lanka. A — *M. magnater* (MHNG 1981.071); B — *M. fuliginosus* (ZMMU S-164504); C — *M. pusillus* (V/M/ERS/570); D — *M. phillipsi* sp. nov. (NMSL 2021.03.01.NH, holotype)

TABLE 5. Dental measurements (mm) of *M. phillipsi* sp. nov. from Idalgashinna, Sri Lanka. Measurements presented as $\bar{x} \pm$ SD, range, and sample size *n*. Measurements of the holotype, paratypes and other individuals of the new species and other species of *Miniopterus* occurring in India and Sri Lanka are shown for comparative purposes. Measurements of *M. phillipsi* sp. nov. were taken by TK, while the other specimens by an assortment of different authors

Specimen or taxon	C–C	M3–M3	C–M3	I1–M3	i1–m3	MOLS	mols
M. phillipsi sp. nov. Holotype ♀, NMSL 2021.03.01.NH	4.65	6.58	6.14	7.29	7.50	5.13	5.58
M. phillipsi sp. nov. Paratype ♂, NMSL 2021.03.02.NH	4.68	6.31	5.97	7.23	7.31	5.02	5.51
M. phillipsi sp. nov. Paratype ♂, NMSL 2021.03.03.NH	4.70	6.56	6.22	7.41	7.60	5.27	5.78
M. phillipsi sp. nov. all specimens	4.65 ± 0.14 4.3–4.9, *22*	6.55 ± 0.09 6.3–6.7, *22*	6.05 ± 0.11 5.8–6.2, *22*	7.22 ± 0.11 7.0–7.4, *21*	7.50 ± 0.15 7.1–7.8, *22*	5.05 ± 0.16 4.7–5.2, *22*	5.73 ± 0.16 5.4–6.0, *22*
M. fuliginosus	4.61 ± 0.19 4.3–4.9, *14*	6.71 ± 0.15 6.4–7.0, *14*	6.18 ± 0.11 6.0–6.4, *14*	7.36 ± 0.10 7.2–7.4, *14*	7.67 ± 0.09 7.5–7.8, *14*	5.04 ± 0.09 4.8–5.1, *14*	5.87 ± 0.21 5.5–6.4, *14*
M. magnater	5.20 ± 0.19 4.8–5.5, *13*	7.37 ± 0.21 7.1–7.7, *13*	6.72 ± 0.10 6.5–6.9, *13*	8.06 ± 0.11 7.9–8.2, *12*	8.31 ± 0.25 7.67–8.72, *12*	5.68 ± 0.11 5.4–5.8, *12*	6.28 ± 0.18 5.9–6.6, *12*
M. pusillus	4.13 ± 0.06 4.0–4.2, *7*	5.77 ± 0.07 5.6–5.8, *7*	5.33 ± 0.07 5.2–5.4, *7*	6.37 ± 0.09 6.2–6.4, *7*	6.72 ± 0.08 6.6–6.8, *7*	4.50 ± 0.01 4.4–4.5, *7*	5.12 ± 0.11 4.9–5.2, *7*

(see e.g. Maeda, 1982), as shown by the overwhelming importance of PC1 in defining *Miniopterus* morphospace.

According to the published records, distribution ranges of *M. magnater* and *M. pusillus* are overlapping with the range of *M. fuliginosus* at the northern parts of South Asia. Further, ranges of *M. phillipsi* sp. nov. and *M. pusillus* are overlapping in Central and South India (Srinivasulu and Srinivasulu, 2012; Saikia, 2018; Ibáñez and Juste, 2019). The historic and current range of *M. phillipsi* sp. nov. in Sri Lanka was assessed by Kusuminda *et al.* (2020) under the name *M.* cf. *fuliginosus*. According to that study, *M. phillipsi* sp. nov. has been recorded from 29 localities representing Central, Uva, Sabaragamuwa, Western, North-western, and Northern provinces of Sri Lanka, although the majority were in the first three provinces. Further, they reported an elevational range of 2–1673 m a.s.l., extending across all three elevation regions (highlands, midlands and lowlands) and all three climatic regions (wet zone, intermediate zone and dry zone) of Sri Lanka (Kusuminda *et al.*, 2020). Prior to the discovery of *M. phillipsi* sp. nov., *M. fuliginosus* sensu lato was recorded from Arunachal Pradesh, Maharashtra, Sikkim, Tamil Nadu, Uttarakhand, West Bengal, Himachal Pradesh, Uttar Pradesh and Kerala in India (Bates and Harrison, 1997; Molur *et al.*, 2002; Saikia, 2018). This range can be split into two subregions: 1) localities in Himachal Pradesh, Uttarakhand, Uttar Pradesh, Sikkim, Arunachal Pradesh, and hilly region of West Bengal resembling the type locality of *M. fuliginosus* in temperate forest biomes and temperate climatic conditions of India (Fig. 3), and 2) locations in Maharashtra and Kerala (Peninsular India) being similar to Sri Lanka in tropical moist forest biome and tropical climatic conditions of India and Sri Lanka (Fig. 3). The presence of *M. phillipsi* sp. nov. in Robbers' Cave demonstrates that this species occurs in southern India. However, a thorough investigation is needed to assess the extent and range limits of *M. phillipsi* sp. nov. in India as well as to determine the southern limits of *M. fuliginosus*. The distribution of the new species in Peninsular India and Sri Lanka also underscores the biogeographic cohesion of the Western Ghats and Sri Lanka Biodiversity Hotspot (Myers *et al*., 2000).

The description of *M. phillipsi* sp. nov. offers a new name for the *Miniopterus* species long known from Sri Lanka, while increasing the number of *Miniopterus* species known from India to four. We also wish to highlight that this is the first *Miniopterus* species to be described from Asia in six decades (Laurie and Hill, 1957; Ruedi *et al.*, 2012*a*) and from India and Sri Lanka in eight decades (Sanborn, 1931). It is also the first bat species to be newly described from Sri Lanka since the golden era of Sri Lankan bat studies led by W. W. A. Phillips nearly a century ago (Phillips, 1922, 1923, 1924, 1932, 1935, 1980). Other additions to island's bat fauna involved species recorded elsewhere from Asia (a hipposiderid by Bates and Harrison, 1997; a pteropodid by Mapatuna *et al.*, 2002; and a vespertilionid by Edirisinghe *et al.*, 2018). Recently, Edirisinghe *et al.* (2018) reported a specimen of

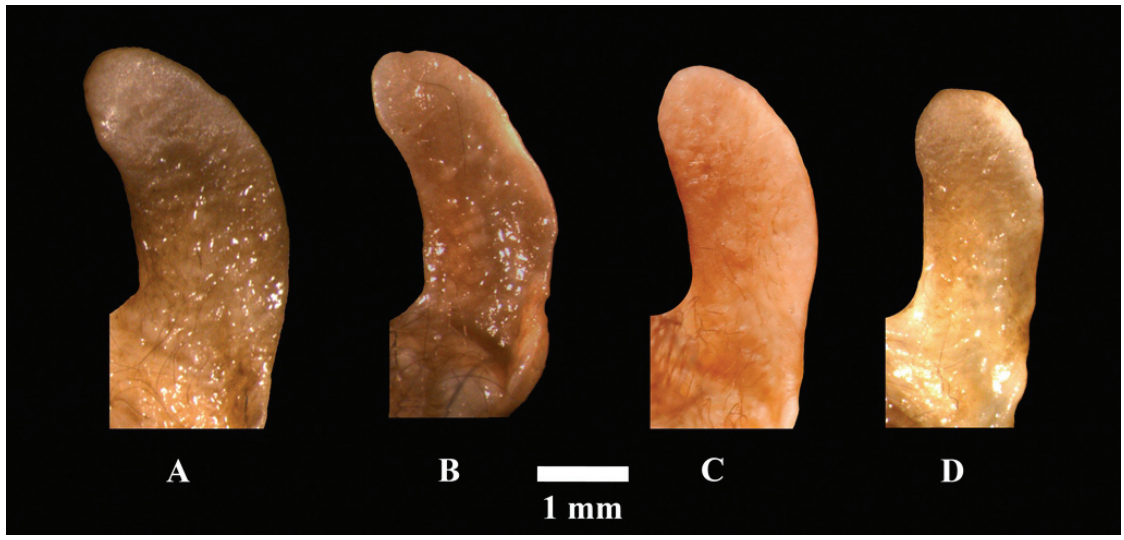

FIG. 8. Tragus of *Miniopterus* species in India and Sri Lanka. A — *M. magnater* (ZMMU S-172585); B — *M. fuliginosus* (ZMMU S-164505); C — *M. phillipsi* sp. nov. (NMSL 2021.03.01.NH, holotype); D — *M. pusillus* (ZMMU S-172595)

Phoniscus cf. *jagorii* in Sri Lanka, based solely on its external morphology. Certainly, molecular analyses and detailed craniodental investigations are warranted to resolve its relationships to known species of *Phoniscus*. In the only previous study to use molecular techniques to assess the taxonomic status of bats in Sri Lanka, Mapatuna *et al.* (2002) confirmed the existence of two distinct species of *Cynopterus* in the country. The use of DNA barcoding and detailed morphological and morphometric analysis has accelerated the rate of species discovery in East and Southeast Asia (Soisook *et al.*, 2015, 2016, 2017; Kuo *et al.*, 2017; Ruedi *et al.*, 2017; Tu *et al.*, 2018; Yu *et al.*, 2020) and to a lesser extent in South Asia (Ruedi *et al.*, 2012*b*; Saikia *et al.*, 2017; Srinivasulu *et al.*, 2018, 2019; Thong *et al.*, 2018; Chakravarty *et al.*, 2020). Genetic studies on Indian and Sri Lankan bats is yet to catch up when compared to those in neighboring regions (Saikia, 2018). Our study highlights the importance of using both morphometric analysis and molecular techniques in taxonomic studies on South Asian bats.

SUPPLEMENTARY INFORMATION

Contents: Supplementary Figures: Fig. S1. Maximum Likelihood consensus tree of the *COI* gene of Asian *Miniopterus* species. Dark circles depict nodes with Bootstrap support ≥ 70; Fig. S2. Landscape of the type locality of *M. phillipsi* sp. nov. i.e., Mountain range at the southern edge of Central Highlands of Sri Lanka at Idulgashinna. Arrow showing the location of cave. Inset image: entrance of the Idulgashinna cave; Fig. S3. Ears of *Miniopterus* species in India and Sri Lanka. A. *M. magnater* (MHNG 1981.071); B. *M. fuliginosus* (V/M/ERS/411); C. *M. phillipsi* sp. nov. (NMSL 2021.03.02.NH, paratype); D. *M. pusillus* (V/M/ERS/570); Fig. S4. Pelage of *M. phillipsi* sp. nov. (NMSL 2021.03.02.NH, paratype). A. dorsal fur color; B. ventral fur color. Supplementary Appendices: Appendix S1. Cytochrome oxidase I (*COI*) sequences of *Miniopterus* species, and out-group, used in this study. Incorrect names assigned for the sequences deposited at GenBank and BOLD were corrected here and incorrect names were mentioned with in brackets; Appendix S2. Data of specimens used in the morphological analyses. Museum acronyms include: NMSL: National Museum of Sri Lanka; NWRTC: National Wildlife Research and Training Centre, Giritale, Sri Lanka; HZM: Harrison Institute (formerly Harrison Zoological Museum); ZMMU: Zoological Museum of Moscow University; HNHM: Hungarian Natural History Museum; MHNG: Muséum d'Histoire Naturelle de Genève; ZSI: Zoological Survey of India; Appendix S3. Results of linear discriminant analysis. Supplementary Information is available exclusively on BioOne.

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