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► **To cite this version:**

Vuong Tan Tu, Tamás Görföl, Gabor Csorba, Satoru Arai, Fuka Kikuchi, et al.. Integrative taxonomy and biogeography of Asian yellow house bats (*Vespertilionidae*: *Scotophilus*) in the Indomalayan Region. *Journal of Zoological Systematics and Evolutionary Research*, In press, 10.1111/jzs.12448 . hal-03113629

HAL Id: hal-03113629

<https://hal.sorbonne-universite.fr/hal-03113629>

Submitted on 18 Jan 2021

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1 **Integrative taxonomy and biogeography of Asian yellow house bats (*Vespertilionidae*:**
2 ***Scotophilus*) in the Indomalayan Region**

3

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59

60 **Running title: Integrative taxonomy and biogeography of Asian *Scotophilus***

61

62

63 **Abstract**

64

65 Yellow house bats (*Scotophilus*) have been known for centuries as a widespread genus of
66 vesper bats in the Indomalayan Region. Despite this, their taxonomic status and
67 phylogeographical patterns remain unclear due to differing criteria employed by early
68 taxonomists and inconsistencies between morphological and molecular assessments. To
69 address these issues, we undertook a comparative phylogeographic analysis of Asian
70 *Scotophilus* spp. using integrated genetic and morphological analyses of samples collected
71 across the region. These demonstrate that yellow house bats in Asia can be classified into just
72 two widespread species, namely the smaller *S. kuhlii* (e.g., FA \leq 53.1 mm, GLS \leq 20.18 mm)
73 and the larger *S. heathii* (e.g., FA \geq 53.4 mm, GLS \geq 20.85 mm), which occur in sympatry in
74 different parts of the Indomalayan Region. Although these two sympatric species share
75 similar eco-ethological preferences, they differ considerably in their geographic distributions
76 and intraspecific variation in mtDNA sequences and morphological traits. These disparities
77 were likely misinterpreted as indicating potential cryptic diversity in previous studies,
78 whereas we suggest they are related to interspecific differences in sex-biased gene flow and
79 phenotypic plasticity to adapt to varying environments. Our study highlights the importance
80 of using multiple datasets to resolve taxonomic uncertainties and reconstruct demographic
81 and phylogeographic histories of sympatric species.

82

83 Keywords: integrative taxonomy, comparative phylogeography, multiple datasets, sympatric
84 species, *Scotophilus*.

85

86 1. Introduction

87

88 Species constitute one of the fundamental units of study in many fields of biology.
89 However, the multiplicity of species concepts and criteria used to delineate species
90 boundaries have led to considerable taxonomic confusion and numerous controversies
91 (Aldhebiani, 2018; de Queiroz, 2005, 2007). A typical example of such confusion concerns
92 the systematics of the genus *Scotophilus* Leach, 1821 (family Vespertilionidae), which
93 comprises yellow house bats that are widely distributed in the Old World tropics.

94

95 Until the third edition of Mammal Species of the World (Wilson & Reeder, 2005),
96 most mammalogists adopted the Biological Species Concept (Mayr, 1942). As such, they
97 usually regarded morphological and ecological variation and/or geographical isolation as
98 indicative of reproductive isolation among sister species and considered that the systematics
99 of mammals were relatively complete and accurate (Baker & Bradley, 2006). Following
100 taxonomic reviews in the 20th century, Simmons (2005) recognised 12 valid species in the
101 genus *Scotophilus*, most of which were polytypic and widely distributed in the Old World
102 tropics. Since this time, exploration of poorly studied regions and development of analytical
103 approaches that integrate morphological, molecular and acoustic data have altered taxonomic
104 opinions regarding the utility of different species concepts and associated criteria for
105 delineating species boundaries, including within *Scotophilus* spp. (Baker & Bradley, 2006;
106 Demos, Webala, Bartonjo, & Patterson, 2018; Francis et al., 2010; Trujillo, Patton, Schlitter,
107 & Bickham, 2009; Vallo & Van Cakenberghe, 2017). For instance, recent integrative studies
108 have revealed that certain traditionally accepted and polytypic species of *Scotophilus* in
109 Africa actually comprise several distinct species which were previously unrecognized or
110 subsumed as subspecies due to their morphological similarities. As a consequence, the
111 number of valid African *Scotophilus* species has increased from eight (Simmons, 2005) to 18
112 and will likely continue to grow as further cryptic forms of widespread taxa are found (Demos
113 et al., 2018; Trujillo et al., 2009; Vallo, Reeder, Vodzak, & Benda, 2019; Vallo & Van
114 Cakenberghe, 2017).

115

116 Prior to 1940, Asian *Scotophilus* included 17 distinct taxa (species and subspecies)
117 (Figure 1; Table S1). Between 1940 and 2000, several studies addressed the taxonomic status
118 of *Scotophilus* spp. in Asia on the basis of their morphology (Table 1). These led to consensus
119 among early bat taxonomists that two sizes of yellow house bats, small and large, co-occur in

120 many parts of the Indomalayan Region (Corbet & Hill, 1992; Hill & Thonglongya, 1972;
121 Shamel, 1942; Siddiqi, 1960; Tate, 1942). However, these studies frequently employed
122 differing criteria to interpret morphological variation in their specimen material and
123 consequently applied different taxonomic approaches to the same geographical populations. A
124 typical example of this is apparent in the differences in the systematics of the two yellow
125 house bats present in the Sunda Islands (e.g. Java, Bali, Belitung and Borneo).

126
127 Within the Sunda Islands, Tate (1942) included all specimens of yellow house bats
128 collected on Java and nearby islands in three subspecies of *S. temminckii* Horsfield, 1824 (= *S.*
129 *kuhlii* Leach, 1821; see Hill & Thonglongya, 1972): *S. t. temminckii*, *S. t. collinus* Sody, 1936
130 and *S. t. solutatus* Sody, 1936. In contrast, Shamel (1942) classified the small and large
131 yellow house bats on Java into two distinct species, *Pachyotus* (= *Scotophilus*) *temminckii* and
132 *P. solutatus*, respectively. The taxonomic situation became more complex when Siddiqi
133 (1960) also classified Javanese yellow house bats into two species, the smaller *S. t.*
134 *temminckii* and the larger *S. heathii* Horsfield, 1831. However, specimens of the larger
135 species and females of the smaller taxon recognized by Siddiqi (1960) were morphologically
136 comparable to those of *P. solutatus* (*sensu* Shamel, 1940). Likewise, Corbet & Hill (1992)
137 allocated Asian *Scotophilus* into just two polytypic species, namely (1) *S. kuhlii*, including
138 subspecies/synonyms occurring widely in the Indomalayan Region: *castaneus* Horsfield,
139 1851, *collinus*, *consobrinus* Allen, 1906, *fulvus* Gray, 1843, *gairdneri* Kloss, 1917,
140 *panayensis* Sody, 1928, *solutatus*, *swinhoei* Blyth, 1860, *temminckii*, and *wroughtoni*
141 Thomas, 1897; and (2) *S. heathii*, including the synonyms *belangeri* Geoffroy L., 1834,
142 *flaveolus* Horsfield, 1851, *insularis* Allen, 1906, *luteus* Blyth, 1851 and *watkinsi* Sanborn
143 1952 which were restricted to mainland Asia, plus *celebensis* Sody, 1928 endemic to
144 Sulawesi. This view ignored the treatments of Shamel (1942) and Siddiqi (1960) in
145 considering all yellow house bats on Java and nearby islands as representatives of *S. kuhlii*
146 *sensu lato* (s.l.) and created extensive overlap in the morphology of bats of this taxon (i.e. FA:
147 45–59 mm) and those of *S. heathii* s.l. (i.e. FA \geq 55 mm) (Figure 1; Table 1).

148
149 Contrary to earlier treatments (Corbet & Hill, 1992; Shamel, 1942; Siddiqi, 1960;
150 Tate, 1942), Kitchener, Packer, & Maryanto (1997) argued that smaller *Scotophilus* with a FA
151 of less than 54 mm on the Greater (Java and Borneo) and Lesser Sunda Islands were readily
152 identifiable as two distinct species, namely the smaller *S. collinus* (i.e. mean FA values for
153 males and females: 49.1 and 50.9 respectively) and the larger *S. kuhlii* (i.e. mean FA values

154 for males and females are 51.8 and 52.5, respectively). Both of these species were further
155 divided into two morphological forms, but only those of the larger species, *S. kuhlii* s.l. were
156 regarded as two subspecies, namely *S. k. temminckii* inhabiting West and East Java and its
157 relatively smaller sister *S. k. solutatus*, occurring on East Java and Bali. On East Java, two
158 subspecies of *S. kuhlii* were recognised in adjacent mountain ranges separated by the
159 Bondoyudo River plains, and the authors even suggested that they might be distinct species.

160

161 In light of the above, the taxonomic status of several subspecies or races of two
162 polytypic species, *S. kuhlii* s.l. and *S. heathii* s.l. (*sensu* Corbet & Hill, 1992) is likely
163 inaccurate. Many of these taxa were originally described as distinct species or subspecies that
164 were individually distinguished by certain morphological variation (pelage colour or body
165 size) and/or geographical hiatus (Figure 1; Table S1). Nonetheless, Simmons (2005) and
166 subsequent authors (Hutson, Kingston, Francis, & Suyanto, 2008; Moratelli et al. 2019;
167 Sinaga & Maryanto, 2008; Srinivasulu & Srinivasulu, 2019a, 2019b) recognised only four
168 distinct species of Asian *Scotophilus*: (1) *S. kuhlii*, found widely in the Indomalayan Region;
169 (2) *S. collinus*, occurring sporadically in the Greater and Lesser Sunda Islands; (3) *S. heathii*,
170 found in mainland Asia, except for the southern Indochinese subregion; and (4) *S. celebensis*,
171 endemic to Sulawesi (Figure 1). Among these, the separation of *S. celebensis* from *S. heathii*
172 was regarded as provisional (Simmons, 2005) because it was based solely on the disjunct
173 distributions of the two taxa (Corbet & Hill, 1992; Tate, 1942).

174

175 Recent genetic studies have improved our understanding of the taxonomy and
176 biogeography of Asian yellow house bats (Francis et al., 2010; Hisheh, How, Suyanto, &
177 Schmitt, 2004; Trujillo et al., 2009; Yu, Chen, Li, & Wu, 2012). In relation to morphological
178 taxonomy, the separation of the two differently sized species, *S. kuhlii* and *S. heathii*, has been
179 highly supported by genetic analyses (Francis et al., 2010; Trujillo et al., 2009). Within *S.*
180 *kuhlii* s.l., all recent studies have found little genetic differences between geographically
181 distant populations in the Lesser Sunda Islands (Hisheh et al., 2004), from Vietnam,
182 Peninsular Malaysia and the Philippines (Trujillo et al., 2009), from northern and southern
183 Indochina (Laos and Vietnam) (Francis et al., 2010) and from Hainan Island and mainland
184 China (Yu et al., 2012). These data indicate that gene flow across the studied populations of *S.*
185 *kuhlii* has not been limited by geographical distance or sea-barriers (Hisheh et al., 2004; Yu et
186 al., 2012). While comparable morphological data are still lacking due to inadequate or
187 disparate sampling, it is very likely that *S. kuhlii* represents a monotypic species. For this

188 reason, research is needed to confirm the taxonomic validity of species or subspecies that
189 were subsumed into or distinguished from *S. kuhlii* on the basis of morphology alone.

190

191 Compared to *S. kuhlii* s.l., *S. heathii* s.l. has similar eco-ethological preferences.
192 However, the latter species may have a greater dispersal ability due to its higher wing loading
193 and aspect ratio e.g. 15 vs 11.6 and 8.0 vs 6.96, respectively (Francis, 2008; Luo et al., 2019;
194 Norberg & Rayner, 1987; Zhu, Chmura, & Zhang, 2012). If so, this would suggest that *S.*
195 *heathii* s.l. could also maintain a strong gene flow between its geographically distant
196 populations. This inference is supported by Trujillo et al. (2009) who analysed genetic
197 divergences in mtDNA (*Cytb*) and nuDNA (zinc finger Y – *zfy* gene) sequences between *S.*
198 *heathii* from Yunnan (China) and northern and southern Vietnam and suggested that these
199 represent the same species. Conversely, Francis et al. (2010) found that *S. heathii* bats from
200 northern Indochina (northern Vietnam and Laos) and southern Indochina (southern Vietnam)
201 constituted two highly divergent clusters of *COI* gene sequences. Because comparable *COI*
202 divergence exist between many closely related species in the Vespertilioninae, Francis et al.
203 (2010) suggested that Indochinese *S. heathii* may represent a complex of different species.
204 However, since mitochondrial data are maternally inherited, they should not be solely used to
205 draw taxonomic conclusions (Dool et al., 2016; Hassanin, An, Ropiquet, Nguyen, & Couloux,
206 2013; Nesi, Nakouné, Cruaud, & Hassanin, 2011; Tu et al., 2017; Tu, Hassanin, Furey, Son,
207 & Csorba, 2018). For a more integrative approach, the hypothesis of Francis et al. (2010)
208 requires further testing with biparental genetic markers, geographically denser sampling and
209 additional morphological data.

210

211 This paper presents a phylogeographic study of Asian *Scotophilus* based on new
212 specimens obtained from different areas in the Indomalayan Region. To this end, we integrate
213 genetic and morphological analyses to (1) address taxonomic uncertainties (e.g.
214 misidentifications or potential cryptic diversity) regarding Asian yellow house bats; (2)
215 evaluate patterns in the demographic and evolutionary histories of species recognized by this
216 study; and (3) consider the roles of ecological factors in shaping the current distributions,
217 population genetic structures and morphological variation of the species. Our overall aim was
218 to improve understanding of the taxonomy and biogeography of Asian yellow house bats.

219

220 **2. Materials and Methods**

221

222 **2.1. Taxonomic sampling**

223

224 In this study, we examined 106 bats of *S. kuhlii* s.l. (n=76) and *S. heathii* s.l. (n=30)
225 collected from different parts in the Indomalayan Region (Figure 1; Appendix 1). Of which,
226 97 voucher specimens are held in the Institute of Ecology and Biological Resources (IEBR,
227 Hanoi, Vietnam), the Hungarian Natural History Museum (HNHM, Budapest, Hungary), the
228 Centre for Biodiversity Conservation (CBC, Royal University of Phnom Penh, Cambodia),
229 the University of Tokyo Hokkaido Forest (UTHF, Furano, Hokkaido, Japan), and the
230 University of the Philippines Los Banos Museum of Natural History (UPLB-MNH, Laguna,
231 Philippines) (See Appendix 1). Tissue samples were collected from the chest muscles of
232 voucher specimens or from the patagium (biopsy punches; 3 mm diameter) of released
233 individuals and preserved in 95% ethanol and stored at -20°C.

234

235 We generated 38 *Cytb* (complete cytochrome b; 1,140 bp) and 43 *COI* (fragment of
236 cytochrome c oxidase subunit I; 705-1554 bp) sequences from 49 examined individuals
237 encountered during field surveys undertaken by the authors between 2008 and 2019 (30
238 specimens were sequenced for both mitochondrial genes) (Appendix 1). These newly
239 generated sequences were compared to the 20 *Cytb* and 41 *COI* sequences available in
240 GenBank for Asian *Scotophilus* spp. collected from other localities in the Indomalayan
241 Region by other authors (Figure 1; Table S2) to explore their phylogeographic and
242 phylogenetic relationships. We further sequenced two nuclear genes including intron 9 of
243 *TUFM* (elongation factor Tu, mitochondrial precursor) and intron 6 of *ZFYVE27* (zinc finger,
244 FYVE domain containing 27) for six selected specimens of *S. kuhlii* (n=2) and *S. heathii*
245 (n=4) to test any incongruence between mitochondrial and nuclear DNA phylogenies. Based
246 on previous studies (Roehrs, Lack, & Van Den Bussche, 2010; Trujillo et al., 2009), *Murina*
247 *cyclotis* Dobson, 1872 of the subfamily Murininae and *Eptesicus pachyomus* Dobson, 1871 of
248 the subfamily Vespertilioninae were chosen as outgroups in phylogenetic analyses. Genetic
249 sequences available for these outgroup species in GenBank are indicated in Table S2.

250

251 **2.2. Genetic analyses**

252

253 *DNA extraction, amplification, sequencing*

254

255 Total DNA was extracted from tissue samples using the QIAGEN DNAeasy Tissue
256 Kit (Qiagen, Hilden, Germany) according to the manufacturer's protocol. Primer sets used for
257 PCR amplification of *Cytb* were Mt-14724F/Cyb-15915R (Irwin, Kocher, & Wilson, 1991),
258 Cyb-14726F/Cyb-15909R (Arai et al., 2016) and for *COI* were UTyrLA/C1L705 (Hassanin et
259 al., 2012) or MammMt-5533F/MammMt-7159R (Arai et al., 2019) and for *TUFM* and
260 *ZFYVE27* were TUFM-EX9U/TUFM-EX10L and ZFYVE27-EX6U/ZFYVE27-EX7L,
261 respectively (Hassanin et al. 2013) (See Table S3 for more details).

262

263 Amplifications were done in a volume of 20 μ l including 3 μ l of Buffer 10X with
264 $MgCl_2$, 2 μ l of dNTP (6.6 mM), 0.12 μ l of Taq DNA polymerase (2.5 U, Qiagen, Hilden,
265 Germany) and 0.5–1 μ l of the two primers at 10 μ M. The standard PCR conditions were as
266 follows: 4 min at 95°C; 5 cycles of denaturation/annealing/extension with 45 s at 95°C, 1 min
267 at 60°C and 1 min at 72°C, followed by 30 cycles of 30 s at 95°C, 45 s at 55°C, and 1 min at
268 72°C, followed by 10 min at 72°C. PCR products were resolved by electrophoresis on a 1.5%
269 agarose gel stained with ethidium bromide and visualized under UV light.

270

271 Both strands of PCR products were sequenced using Sanger sequencing on an ABI
272 3730 automatic sequencer at the Centre National de Séquençage (Genoscope) in Evry
273 (France) and ABI 3730xl DNA Analyzer at the Infectious Disease Surveillance Center, Japan.
274 The sequences were edited and assembled using CodonCode Aligner Version 3.7.1
275 (CodonCode Corporation) and Genetyx v11 software (Genetyx Corporation, Japan).
276 Heterozygous positions (double peaks) of nuclear gene sequences were scored using the
277 IUPAC ambiguity codes. Sequences generated for this study were deposited in the
278 EMBL/DDBJ/GenBank database under the accession numbers MT820574-MT820611,
279 MT820613-MT820624, MT820574-MT820611 (Appendix 1).

280

281 *Phylogeographic analyses using mtDNA sequences*

282

283 The number of haplotypes, haplotype diversity (h), and nucleotide diversity (π) for the
284 two nominal species, *S. kuhlii* s.l. and *S. heathii* s.l., were calculated from the alignments of
285 82 *COI* (576 bp) and 58 *Cytb* (1140 bp) sequences (Alignments S1 and S2) using DNASP
286 v5.10 (Librado & Rozas, 2009). Maximum parsimony haplotype networks were reconstructed
287 using the TCS algorithm in PopArt (Leigh & Bryant, 2015). Following this, a hierarchical
288 analysis of molecular variation (AMOVA) (Excoffier, Smouse & Quattro, 1992) was

289 performed with 1,000 permutations in Genodive v.3.0 (Meirmans & Tienderen, 2004) to
290 quantify the genetic variation within and among groups in the TCS network.

291

292 *Phylogenetic reconstruction*

293

294 Phylogenetic trees of Asian *Scotophilus* spp. were reconstructed from DNA
295 alignments (Alignments S3-S7) using Bayesian Inference (BI) and Maximum-Likelihood
296 (ML) methods. DNA sequences were aligned with Aliview v. 1.25 (Larsson, 2014). No gaps
297 and stop codons were found in the alignments of the mitochondrial *COI* and *Cytb* protein-
298 coding genes. In contrast, a few gaps were included in the alignments of the nuclear genes,
299 but their positions were not ambiguous. The indels (insertion or deletion) shared by at least
300 two taxa in the alignments of each nuclear gene were coded as additional characters (“1”:
301 insertion; “0”: deletion) and analysed as a separate partition in the Bayesian analyses. The
302 models of nucleotide evolution were selected under jModelTest V. 2.1.7 (Posada, 2008) using
303 the Akaike Information Criterion (AIC): GTR+G for *COI* dataset, GTR+I for *Cytb* dataset,
304 and HKY model for *TUFM* and *ZFYVE27* datasets. The BI analyses were conducted with
305 MrBayes v. 3.2.5 (Ronquist et al., 2012) using five separate datasets: (1) *COI* (48 sequences;
306 657 bp), (2) *Cytb* (39 sequences; 1140 bp), (3) *TUFM* (642 bp and 10 indels; 8 sequences),
307 *ZFYVE27* (734 bp and 7 indel; 8 sequences) and (5) nuDNA (combining two nuclear genes;
308 1376 bp and 17 indels, 8 sequences) (Alignments S3-S7). The posterior probabilities (PP)
309 were calculated using four independent Markov chains run for 10^7 Metropolis-coupled
310 MCMC generations, with trees sampled every 1000 generations and a burn-in of 25%. The
311 ML analyses of *COI*, *Cytb*, and nuDNA datasets (Alignments S3, S4, and S7) were conducted
312 with W-IQ-TREE tool available online (<http://iqtree.cibiv.univie.ac.at/>) (Hoang et al., 2018;
313 Nguyen et al., 2015; Trifinopoulos et al., 2016) with 1,000 ultrafast bootstrap replicates.
314 Pairwise genetic distances between divergent phylogenetic lineages or TCS clusters were
315 calculated with PAUP* v. 4b10 (Swofford, 2003) using the uncorrected p-distance.

316

317 *Isolation by distance (IBD)*

318

319 Geographic distances (km) between geographic haplogroups of *S. kuhlii* s.l. and *S.*
320 *heathii* s.l. were generated using Geographic Distance Matrix Generator v.1.2.3 (Ersts, 2020).
321 We tested for correlations between pairwise mtDNA distances (minimum p- distance) and
322 geographic distances with the Mantel test (Mantel, 1967) using the generalized linear model

323 in PAST 3.07 (Hammer, Harper, & Ryan, 2001). We also tested for correlations between
324 pairwise genetic distance ($F_{ST}/(1-F_{ST})$) and geographic distance (ln km) for three geographic
325 haplogroups of *S. heathii* identified in the *COI* network.

326

327 *Historical demography*

328

329 The dynamics of effective female population size within *S. kuhlii* s.l. and *S. heathii* s.l.
330 were estimated from the Bayesian skyline plot (BSP) method in BEAST v.2.5.2 (Bouckaert et
331 al., 2019) using *COI* datasets (Alignment S1). As no calibration point (fossil record or
332 biogeographic event) was available for *Scotophilus*, we used a mutation rate of 2×10^{-8} per site
333 per million years for the *COI* gene based on previous studies (i.e. Tu et al. 2017; Mao et al.
334 2010). The model of evolution of *COI* dataset was selected by jModelTest. We ran a MCMC
335 chain of 20 million generations, sampled every 1000 generations and a burn-in of 10% with
336 uncorrelated lognormal relaxed molecular clock. Tracer v.1.6 (available in the BEAST
337 package) was used to assess the adequacy of chain mixing and MCMC chain convergence
338 using ESS values of >200 and to visualize the Bayesian skyline plots.

339

340 **2.3. Morphological analyses**

341

342 *Morphological comparison*

343

344 Ninety-seven *Scotophilus* specimens listed in the Appendix 1 were included in our
345 morphological analyses. All of the specimens examined were adults, as confirmed by the
346 presence of fully ossified metacarpal-phalangeal joints.

347

348 External measurements were taken to the nearest 0.1 mm from alcohol-preserved
349 specimens. These included: FA—length of forearm, Tib—tibia length, from the knee joint to
350 the ankle. Craniodental measurements were taken to the nearest 0.01 mm using digital
351 calipers under a stereomicroscope. These included: GSL—total length of skull, from the most
352 anterior part of the upper incisors to the occiput; SL—greatest length of skull, the anterior rim
353 of the alveolus of the 1st upper incisor to the most posteriorly projecting point of the occipital
354 region; CBL—condylobasal length, from the occipital condyles to the anterior of the alveolus
355 of the 1st upper incisor; CCL—condylo-canine length, from the exoccipital condyle to the
356 most anterior part of the canine; ZB—greatest width of the skull across the zygomatic arches;

357 C¹C¹—greatest width across the upper canines between their buccal borders; M³M³—greatest
358 width across the crowns of the last upper molars; CM³—maxillary toothrow length, from the
359 anterior of the upper canine to the posterior of the crown of the 3rd upper molar; ML—length
360 of mandible, from the anterior rim of the alveolus of the first lower incisor to the most
361 posterior part of the condyle; and CM₃—mandibular toothrow length, from the anterior of the
362 lower canine to the posterior of the crown of the 3rd lower molar.

363

364 In this study, we initially assigned our study specimens to different groups based on
365 molecular data. Specimens lacking genetic information were classified into molecular groups
366 according to their geographic origin (Figure 1). As specimens examined within these groups
367 lacked sexual dimorphism in all external and craniodental measurements (T-test, $p > 0.05$), the
368 phenetic affinity of the identified taxa with both sexes combined was inferred through
369 univariate and multivariate analyses of their morphometrics. Principal Component Analysis
370 (PCA) of study specimens was undertaken in PAST 3.07 (Hammer et al, 2001) using 10 log-
371 transformed craniodental measurements. Equalities of mean values of morphometrics and PC
372 scores among different taxa were tested using a one-way analysis of variance (ANOVA),
373 followed by a post-hoc Tukey HSD multiple comparison test for unequal sample sizes
374 (Tukey-Kramer) (Zar, 1999).

375

376 3. RESULTS

377

378 3.1. Genetic analyses

379

380 3.1.1. Phylogeographic patterns of Asian *Scotophilus* inferred from mtDNA sequences

381

382 In the *COI* alignment (576 bp), 22 haplotypes were identified among 43 individuals of
383 *S. kuhlii* s.l., and 18 haplotypes among 39 individuals of *S. heathii* s.l.. In the *Cytb* alignment
384 (1,140 bp), 27 haplotypes were identified among 46 bats of *S. kuhlii* s.l. and seven among 12
385 bats of *S. heathii* s.l. (Figure 1; Appendix 1; Table S2). Haplotype (Hd) and nucleotide
386 diversities (π) calculated from *COI* and *Cytb* alignments for the entire populations of each
387 taxon were high i.e. >0.86 and >0.01 , respectively (Table S4). In both species, most
388 individuals examined, even those from the same locations, carried unique *COI* or *Cytb*
389 haplotypes.

390

391 The *COI* and *Cytb* networks reconstructed for *S. kuhlii* s.l. and *S. heathii* s.l. have a
392 “bush-like” shape without ancestral haplotype (Figure 1). However, mtDNA haplotypes
393 derived from geographically distant populations of *S. kuhlii* s.l. were found to be intermixed
394 or identical, whereas those of *S. heathii* s.l. displayed geographical patterns. For instance, the
395 *COI* TCS network shows the separation of three clusters of haplotypes derived from
396 individuals of *S. heathii* s.l. collected in: (1) Indian Subcontinent, including those collected
397 from locations 1–3 in Pakistan and location 4 in India; (2) southern Indochina, including those
398 found from locations 16–21; and (3) northern Indochina, including samples found from
399 locations 9–12. AMOVA analyses revealed that pairwise genetic distances (F_{st}) among these
400 three clusters were between 0.11–0.433 and significant (Table S5). Likewise, in the *Cytb* TCS
401 network, the private haplotypes found in three geographic areas (Yunnan (China), northern
402 and southern Vietnam (or Indochina) were also separated (Figure 1).

403

404 Consistent with the observed divergences in phylogeographic patterns between the
405 two species, Mantel tests (Figure S1A) showed a lack of statistically significant correlations
406 between pairwise mtDNA and geographic distances in *S. kuhlii* s.l. (correlation $R^2 < 0.3$) and
407 the opposite in *S. heathii* s.l. ($R^2 \geq 0.66$) (Figure S1A). Similarly, the genetic differentiation
408 among three geographic haplotype clusters of the latter taxon obtained from *COI* network
409 analysis largely resulted from IBD effects (Table S5; Figure S1B).

410

411 3.1.2. Phylogeny of the Asian *Scotophilus* inferred from mtDNA sequences

412

413 The phylogenetic trees reconstructed from the alignments of mtDNA genes (*COI* and
414 *Cytb*) are depicted in Figures 2 and S2. The genus *Scotophilus* and the two species *S. kuhlii*
415 s.l. and *S. heathii* s.l. were monophyletic in all phylogenetic analyses with maximal support
416 (PP/BP=1/100). Interspecific distances (uncorrected p-distance) calculated from *COI* and
417 *Cytb* datasets between these nominal species were $\geq 13.9\%$ and $\geq 14.5\%$ respectively (Table 2).

418

419 Within *S. kuhlii* s.l., all *COI* and *Cytb* trees included bats from different geographic
420 areas or subunits of the Indomalayan Region i.e. (1) India and Myanmar, (2) Indochina
421 (Cambodia, Laos, Vietnam) and southern China, (3) Peninsular Malaysia, and (4) the
422 Philippines intertwined with a maximum intraspecific genetic divergence (p-distance)
423 calculated from *COI* and *Cytb* sequences of $\leq 2.3\%$ (Figures 2a–b and S2; Table 2).

424

425 Within *S. heathii* s.l., our *COI* trees (Figures 2a and S2) recovered four lineages, A, B,
426 C, and D. Haplotypes from southern Indochina appeared in lineages A (comprising those
427 collected from locations No. 16, 17, 19, 20 and 21 in Figure 1) and B (those collected from
428 location No. 18 in Figure 1), whereas haplotypes from northern Indochina and the Indian
429 Subcontinental (India and Pakistan) formed two sister lineages, C and D respectively. The
430 range of pairwise p-distances estimated from *COI* sequences between lineages A and B were
431 1.1–2.3%, 2.6–4.0% between C and A+B, 5.1–7.1% between C and D, and 5.2–7.6% between
432 A+B and D. The maximum intraspecific variation within these lineages (i.e. lineage A) was
433 $\leq 1.6\%$ (Table 2). Likewise, in our *Cytb* tree (Figures 2b and S2), a single individual from
434 Yunnan (China) occupied a basal position to a clade (PP/BP=1/93) united by two well-
435 supported sister lineages, one containing haplotypes in northern Vietnam (=lineage C; Figure
436 2a) and the other containing haplotypes from southern Vietnam (=lineage A; Figure 2a)
437 (PP/BP=1/97-100). The range of p-distances calculated from *Cytb* sequences between these
438 three lineages was 3.7–4.2%, whereas those within populations in northern and southern
439 Vietnam were $\leq 1\%$ (Table 2).

440

441 3.1.3. Phylogeny of Indochinese *Scotophilus* based on nuDNA sequence analyses

442

443 Bayesian trees reconstructed from three nuDNA datasets i.e. *TUFM*, *ZFYVE27* and
444 concatenation of the two nuDNA introns from selected individuals of *S. kuhlii* and *S. heathii*
445 from the northern and southern Indochinese geographical units, as revealed by analyses of
446 mtDNA sequences, are presented in Figures 2c, S2 and S3, respectively. Consistent with
447 mtDNA trees, the nuDNA trees supported the monophyly of *Scotophilus* and the two nominal
448 species, *S. kuhlii* and *S. heathii*, with maximum robustness (PP/BP=1). More specifically, in
449 the *TUFM* and *ZFYVE27* sequence alignments, all *Scotophilus* bats examined shared a total of
450 8 and 3 indels respectively, whereas *S. kuhlii* and *S. heathii* were diagnosed by several indels
451 (Figure 2c). Likewise, and inconsistent with mtDNA trees, the substructure of geographical
452 populations in *S. heathii* were not recovered in our analyses of separated or combined nuDNA
453 sequences (Figures 2c and S2). The genetic distances calculated from concatenation of the
454 two nuclear introns (i.e. the p-distances) between *S. kuhlii* and *S. heathii* ranged between 1.4
455 and 1.6%, whereas the nuDNA sequences of selected bats of both species from different
456 geographical units were identical (p-distances $< 0.1\%$) (Table 2).

457

458 3.2. Historical demography

459

460 Our Bayesian skyline plot (BSP) analyses indicated that populations of both *S. kuhlii*
461 and *S. heathii* have maintained their long-term stability since the Mid-Late Pleistocene (ca.
462 1.5-0.5 million years ago (Mya) and experienced rapid expansion since ca. 0.3 Mya (Late
463 Pleistocene). However, since 0.1 Mya of the late Pleistocene, the total effective population
464 size of *S. kuhlii* was always larger than *S. heathii* (Figure S4).

465

466 **3.3. Morphological analyses**

467

468 Asian *Scotophilus* are relatively large vespertilionids which share similar
469 morphological characteristics: i.e. moderately-sized ears; tragus very long and narrow,
470 tapering slightly towards tip and curving forwards; skulls thick and heavily-built, with just
471 one pair of large, well-developed upper incisors; dental formula I1/3, C1/1, P1/2, M3/3
472 (Figures 3 and 4) (Corbet & Hill, 1992; Dobson, 1875; Tate, 1942).

473

474 Both univariate and multivariate analyses of morphological characters revealed a large
475 individual originally identified as *S. kuhlii* from Java (Indonesia) (HNHM 2869.22) as an
476 extreme outlier, distantly related to other specimens of *S. kuhlii* sensu stricto (s.s.) but
477 resembled our specimens of *S. heathii* s.s. (Figure 5; Table 3). As genetic data were not
478 available and its external and craniodental characters matched those of *S. ? solutatus* s.s.
479 (*sensu* Tate, 1942; Shamel, 1942), this Javanese specimen was treated as a separate taxon in
480 subsequent analyses. Accordingly, *S. kuhlii* s.s. differs from *S. heathii* s.s. in its smaller body
481 and skull size: i.e. FA: 45.7–53.1 vs 54.3–66.0 mm and GSL: 18.30–20.18 vs 20.85–25.20
482 mm (Table 3; Figure 5; Table S6). Aside from the presence of a well-developed occipital
483 helmet in *S. heathii* s.s., the skull morphology of both species is similar (Figure 4; Table 3).
484 As shown in Figure 3, species identification of Asian yellow house bats based solely on
485 pelage colour should be cautiously interpreted due to geographical variation. Although pelage
486 colour is useful for distinguishing taxa living in sympatry, the reliability of this trait seems
487 doubtful for comparing specimens from different countries, and it is entirely inaccurate for
488 museum specimens due to fading of colour during preservation.

489

490 Within *S. kuhlii* s.s., specimens from mainland Asia (India, Myanmar, Indochina,
491 Peninsular Malaysia) and the Philippines overlapped significantly in body and skull size
492 (Figure 5; Table 3). Likewise, within *S. heathii* s.s., separation between specimens initially

493 allocated to different mtDNA lineages was lacking, although local differentiations were
494 recovered in phenotypes among bats of pairwise geographic populations, even at fine scales
495 (Figure 5; Table 3). For instance, bats of *S. heathii* s.s. in southern Indochina appeared in
496 three different morphological subgroups according to body and skull size i.e. with a FA of
497 54.3 to 66.0 mm or a GSL of 20.85 to 25.20 mm, respectively (ANOVA, $p \leq 0.05$; Table S7):
498 (1) smaller bats in south-central Vietnam (location No. 21 and adjacent area, Figure 1); (2)
499 intermediate bats in north-eastern Cambodia (location No. 18, Figure 1); and (3) larger bats in
500 the central highlands of Vietnam (location No. 19, Figure 1) (Figure 5). Similarly, in the PCA
501 of craniodental characters (Figure 5), *S. heathii* s.s. bats in the Indian Subcontinent and
502 southern Indochina were separated by PC2 which is significantly correlated with the greatest
503 width across the upper canines (C^1C^1) (Table S6).

504

505 4. Discussion

506

507 4.1. Cryptic diversity or inadequate taxonomy?

508

509 Early taxonomists differed considerably in how they delineated species boundaries
510 between taxa allocated to *S. kuhlii* s.l. and *S. heathii* s.l. (*sensu* Corbet & Hill, 1992) in the
511 Indomalayan Region, especially those found on the Sunda Islands (Table 1). According to our
512 integrated analyses, *S. kuhlii* s.s. and *S. heathii* s.s. are genetically and morphologically
513 distinct species. The former species is monotypic whereas the latter one is likely polytypic. In
514 particular, FA—a standard measurement with low variation among bat researchers—appears
515 to be reliable for differentiating the two species, as indicated by our PCAs on craniodental
516 traits (Figures 5 and S5). Pairwise comparisons of FA data in different studies (Figure 6)
517 show that apart from some larger individuals in Java and nearby islands (Belitung and
518 Borneo), all other bats assigned to *S. kuhlii* s.l. in the Indomalayan Region are
519 morphologically comparable to our *S. kuhlii* s.s. (i.e. $FA \leq 53.1$ mm). This includes *S. collinus*
520 (*sensu* Kitchener et al., 1997) which we regarded as a member of *S. kuhlii* in agreement with
521 previous authors (e.g. Corbet & Hill, 1992; Shamel, 1942; Tate, 1942). Regarding the larger
522 specimens of *S. kuhlii* s.l. (i.e. $FA \geq 53.4$ mm) from Java, Belitung and Borneo, some were
523 identified as *S. k. temminckii* in past studies (Kitchener et al., 1997; Siddiqi, 1960; Sody,
524 1928, 1936), whereas others were identified as *S. k. collinus* and *S. k. solutatus* (Sody, 1936;
525 Tate, 1942). These controversial specimens and those of *S. heathii* s.l. in mainland Asia and
526 Java (Shamel, 1942; Siddiqi, 1960; Tate, 1942), *S. ? celebensis* in Sulawesi (Sody, 1928;

527 Tate, 1942), and *P. solutatus* (= *S. solutatus*) in Java (Indonesia) (Shamel, 1942) are
528 comparable to our specimens of *S. ? solutatus* s.s. and *S. heathii* s.s. (Figure 6; Tables 1 and
529 3). The new evidence from our study suggests that the current taxonomy of Asian *Scotophilus*
530 spp. (i.e. Moratelli et al. 2019; Simmons, 2005) is inaccurate.

531

532 Kitchener et al. (1997) assigned yellow house bats with forearm lengths of ≤ 54 mm
533 from the Sunda Islands to either *S. collinus* s.s. or *S. kuhlii* s.s. depending on body size i.e. the
534 mean FA values for males / females of each taxon were 49.1 / 50.9 and 51.8 / 52.5,
535 respectively. Their *a priori* species identifications were then checked by multiple regressions
536 and discriminant function analyses (DFAs) of morphological characters. However, certain
537 issues render the classification of Kitchener et al. (1997) unconvincing. For instance, our
538 pairwise comparison of FA values among the taxa recognised by different authors (Figure 6)
539 reveals that their assumption of the upper limit in forearm length for *S. kuhlii* s.l. was
540 unjustified and that their study materials may have contained misidentified individuals of a
541 larger form (or *S. heathii* s.s / *S. ? solutatus*). Our study and previous taxonomic works (i.e.
542 Hill & Thonglongya, 1972; Shamel, 1942; Tate, 1942) have also confirmed the existence of
543 individual variation in size and pelage among bats of the same *Scotophilus* species found in
544 either sympatry or allopatry. As a consequence, the initial species identification of specimens
545 by Kitchener et al. (1997) was uncertain particularly when considering the extensive overlap
546 in all morphometrics given for their recognised taxa with pooled geographic populations i.e.
547 the range of FA values for males / females of each taxon were 44.6–51.9 / 45.2–52.8 and
548 50.5–54.0 / 50.3–53.7, respectively. In addition to potential misidentification of specimens
549 assigned *a priori*, the sample sizes of these taxa were heavily skewed in the two DFAs of
550 Kitchener et al. (1997) which set apart two putative taxa (i.e. the datasets for males and
551 females of *S. collinus* / *S. kuhlii* were 82 / 10 and 124 / 8, respectively). As such imbalanced
552 datasets tend to produce unsatisfactory classifiers, the classification of *a priori* taxa in these
553 DFAs should be considered doubtful, even if statistically significant (López, Fernández,
554 García, Palade, & Herrera, 2013). Consistent with this, separation between the two *a priori*
555 taxa was not recovered in their DFA of skull characters of both sexes combined (as there is no
556 sexually dimorphic effects on size) using another simulated dataset for *S. collinus* / *S. kuhlii*
557 (i.e. 178 / 19 respectively). In particular, Hisheh et al. (2004) considered that *S. kuhlii* s.l. bats
558 throughout the Lesser Sunda Islands can be treated as a panmictic unit. According to
559 Kitchener et al. (1997), the study area of Hisheh et al. (2004) encompasses two sister species
560 which overlap in size, *S. k. solutatus* and *S. collinus*, i.e. FA values (in mm) of their males /

561 females are 50.3–52.4 / 50.5–52.9 and 44.6–51.9 / 46.4–52.8, respectively. This evidence
562 suggests that the classification of different cryptic species within *S. kuhlii* s.l. in the Sunda
563 Islands by Kitchener et al. (1997) reflected only artificial groups of a single species which
564 resemble our *S. kuhlii* s.s.. The latter taxonomic inference is supported by the high overlap in
565 FA values between different putative species determined by Kitchener et al. (1997) and our *S.*
566 *kuhlii* s.s. (Figure 6). Moreover, from a biogeographical viewpoint, geographical distance
567 and/or marine straits between the Lesser Sunda Islands (=study areas of Hisheh et al. (2004))
568 and other parts in the Indomalayan Region (our study) (Figure 1) cannot be considered as a
569 reliable barrier to long-range dispersal and associated gene flow within this species (Hisheh et
570 al., 2004; Yu et al., 2012; this study).

571
572 Based on *COI* distances of >2%, Francis et al. (2010) suggested that two cryptic
573 species may be recognized in *S. heathii*, one from northern Indochina (haplotype C-h7 in
574 Figure 2a) and the other from southern Indochina (haplotypes A-h11, h14, h15, and h17 in
575 Figure 2a). Our phylogeographic analyses of *COI* sequences from a wider taxonomic
576 sampling (including specimens from Cambodia and Vietnam) do not support this view. For
577 instance, our haplotypes from Indochina fall into three lineages (i.e. A, B and C) (Figures 2a
578 and S2). However, the pairwise p-distances calculated from *COI* sequences between these
579 lineages ranged between 1.1–4.0% and overlapped with their intraspecific variation (i.e.
580 lineages A: 0–1.6%) (Table 2). In particular, the interspecific divergences between our
581 Indochinese lineages (A, B and C) were not supported by either nuDNA or morphological
582 analyses (Figures 2c, S2 and 5; Table 2). This is consistent with the results of Trujillo et al.
583 (2009), in which *S. heathii* bats from Yunnan (southern China), northern Vietnam and
584 southern Vietnam have identical *zfy* gene sequences, whereas they belong to three divergent
585 *Cytb* haplogroups (p-distances: 3.7–4.2%) (Figures 2b and S2; Table 2). Indeed, the absence of
586 structured signals in nuclear datasets may be a consequence of low mutation rates or
587 incomplete lineage sorting of these loci (i.e. Hassanin et al. 2013). However, the mito-nuclear
588 discordance of *S. heathii* may be best explained by female philopatry and male biased
589 dispersers (Arnold & Wilkinson, 2015; Rivers, Butlin, & Altringham, 2005; Tu et al., 2017).
590 As such, the hypothesis of potential cryptic diversity within Indochinese *S. heathii* s.l. can be
591 ruled out. Similarly, the relatively higher genetic divergence of *COI* sequences among two
592 morphologically overlapping populations of *S. heathii* s.l. in spatially distant subregions
593 (Indochina lineages A, B, and C and the Indian Subcontinent lineage D (5.1–7.6% p-
594 distances) (Figures 1–3 and S2; Table 2)) might also be attributable to their potential sex-

595 biased gene flow followed by IBD effects (Figure S1). Thus, while further analyses of
596 samples from the intervening zones (Nabhan & Sarkar, 2012; Zwickl & Hillis, 2002) and/or
597 nuclear markers are needed, the possibility that allopatric speciation events have occurred
598 without morphological changes in the above populations of *S. heathii* s.s. (Bickford et al.,
599 2007; Tu et al., 2017, 2018) would seem very unlikely.

600

601 All larger forms of yellow house bats on Java and nearby islands (i.e. FA values of
602 ≥ 53.4 mm and $GSL \geq 20.5$ mm) were previously referred to as *S. kuhlii* (Corbet & Hill, 1992;
603 Simmons, 2005). However, their taxonomic identity was an issue of debate for many years
604 (Figure 6; Table 1). Having examined one of these controversial specimens from Java
605 (HNHM 2869.22), our results suggest that it resembles *S. heathii* s.s. more than *S. kuhlii* s.s.
606 (Figures 4–6; Table 3). This specimen was collected by the Novara Expedition (1857–1859)
607 and its identity was determined by the British zoologist, Oldfield Thomas (1858–1929). It
608 should be noted that before Hill & Thonglongya (1972) confirmed that *S. kuhlii* should
609 replace *S. temminckii* as the correct name for smaller Asian yellow house bats, *S. kuhlii* was
610 used for larger bats by several taxonomists (Allen, 1906; Osgood, 1932; Shamel, 1942;
611 Thomas, 1897) instead of *S. heathii* which other authors used (Siddiqi, 1960; Tate, 1942)
612 (Table 1). This suggests that the previous allocation of our examined specimen (and *S. ?*
613 *solutatus* s.s.) and the larger *Scotophilus* from Java and nearby islands (i.e. Borneo) as
614 *S. kuhlii* s.l. (*sensu* Corbet & Hill, 1992; Simmons, 2005; Kitchener et al., 1997; Tate, 1942) was
615 misguided. In addition, while research on Asian bats has intensified in recent years, most
616 survey effort has focused on habitats such as tropical forests which support high bat diversity
617 (Kingston, 2010), whereas bats that live commensally with humans are comparatively
618 neglected (Jung & Threlfall, 2016). *Scotophilus* spp. are one of the most common bats in
619 urban-rural habitats but roost in high shelters (e.g. roofs of houses) and forage in open spaces
620 above the effective range of ground-based live-traps (i.e. mist-nets and harp traps) (Bates &
621 Harrison, 1997; Francis, 2008; Hisheh et al., 2004). As such, they are likely under-surveyed in
622 many regions of Southeast Asia (Figure 1). Consequently, the disjunct distribution of large
623 yellow house bats between mainland Asia (or *S. heathii* s.s.) and Sulawesi (*S. celebensis* s.s.)
624 (Figure 1) determined by previous authors (e.g. Corbet & Hill, 1992; Simmons, 2005; Tate,
625 1942) may be due to erroneous naming of voucher specimens and gaps in survey coverage.
626 Alternatively, the separation of *S. celebensis* from *S. heathii* by Simmons (2005) could be
627 regarded as unsubstantiated. Thus, until additional analyses further elucidate their
628 phylogenetic relationships, all large yellow house bats (i.e. FA ≥ 53.4 mm and $GSL \geq 20.5$ mm

629 (Figure 6; Tables 1 and 3) occurring in mainland Asia (*S. heathii* s.s.), Java and nearby islands
630 (*S. ? solutatus*), and Sulawesi (*S. celebensis* s.s.) should be regarded as representatives of a
631 single species: *S. heathii*.

632

633 **4.2. Comparative phylogeography of Asian *Scotophilus* spp.**

634

635 The absence of star-like TCS haplotype networks (Figure 1) and results of BSP
636 analyses (Figure S4) in our study indicate that both *S. kuhlii* and *S. heathii* have maintained a
637 constant or expanding effective population size through time since the Mid-Pleistocene. The
638 distribution and lack of bottlenecks in the evolutionary history of Asian yellow house bats in
639 the Indomalayan Region thus differs strikingly from other co-distributed bat species i.e.
640 bamboo bats (*Tylonycteris* spp.) (Tu et al., 2017), woolly bats (*Kerivoula* spp.) (Khan et al.,
641 2010; Tu et al., 2018), horseshoe bats (*Rhinolophus* spp.) (Mao et al., 2010). This may be
642 attributable to eco-ethological differences (Avise, 2000; Hassanin et al., 2016; Moussy et al.,
643 2013). For example, Asian yellow house bats are strong dispersers and aerial-hawking, open
644 space foragers (Bates & Harrison, 1997; Francis, 2008; Norberg & Rayner, 1987), whereas
645 *Tylonycteris*, *Kerivoula* and *Rhinolophus* spp. have a much weaker dispersal ability because
646 they are mostly forest-dwelling taxa (Khan et al., 2010; Mao et al., 2010; Tu et al., 2017;
647 2018). Thus, unlike forest-dependent species, the dispersal and associated gene flow among
648 geographic populations of Asian *Scotophilus* might be less restricted by physical and
649 ecological barriers (Hisheh et al., 2004; Yu et al., 2012). In addition, while the population
650 structure and dynamics of species with low dispersal capacities were strongly influenced by
651 the past compression and expansion of forests during glacial and interglacial periods in the
652 Pleistocene (Khan et al., 2010; Mao et al., 2010; Tu et al., 2017; 2018) and by current patterns
653 of deforestation (Kingston, 2010), Asian *Scotophilus* spp. may have been less affected by such
654 changes.

655

656 Our comparative phylogeographic analyses show that geographically distant
657 populations of *S. kuhlii* in the Indomalayan Region possess very low genetic and
658 morphological variation, whereas those of *S. heathii* in mainland Asia display divergent
659 mtDNA sequences and phenotypes (see section 4.1 for more detail). As discussed above, the
660 incongruences in phylogeographic patterns of mtDNA genetic diversity between the two
661 sympatric species may be attributable to sex-biased gene flows (Avise, 2000; Slatkin, 1987).
662 More specifically, the phylogenetic signals in our mtDNA and nuDNA datasets for *S. heathii*

663 may be consistent with female philopatry and male-biased dispersal whereas those for *S.*
664 *kuhlii* do not exhibit sex-biased dispersal (Arnold & Wilkinson, 2015; Rivers et al., 2005; Tu
665 et al., 2017). As both species may have maintained gene flows among their populations, the
666 geographic variation observed in external and craniodental traits might reflect their
667 phenotypic plasticity to adapt to selective forces imposed by environmental variability, as
668 well as interspecific competition for common resources in areas of sympatry (Chevin, Lande,
669 & Mace, 2010; Ghalambor, McKay, Carroll, & Reznick, 2007; Lande, 2014; Spaeth, 2009;
670 Tienderen, 1997; Zamudio, Bell, & Mason, 2016).

671

672 The low morphological variation of *S. kuhlii* specimens throughout the Indomalayan
673 Region suggests that the species has maintained a generalist phenotype suited to a variety of
674 environments. By contrast, the morphological variability of *S. heathii* indicates that its
675 geographic populations, even those at small scales, may have evolved plastic phenotypes that
676 suit the particular habitats they inhabit (Chevin et al., 2010; Lande, 2014; Spaeth, 2009;
677 Tienderen, 1997; Zamudio et al., 2016). As such, the generalist populations of *S. kuhlii* may
678 have experienced fewer adverse effects from climate and associated habitat changes than *S.*
679 *heathii*. They may also have had more advantages than *S. heathii* when colonizing and
680 adapting to new habitats (Bonte et al., 2012; Ghalambor et al., 2007; Hollander, Verzijden,
681 Svensson, & Brönmark, 2014; Kelly, Panhuis, & Stoehr, 2012; Lande, 2014; Moussy et al.,
682 2013). These inferences suggest that *S. heathii* bats may be more philopatric to their native
683 areas compared to *S. kuhlii*. If so, this would explain how *S. kuhlii* can occupy a wider
684 geographic range in the Indomalayan Region relative to *S. heathii* (Figure 1), even though *S.*
685 *heathii* would be expected to have greater dispersal ability based on its wing morphology.

686

687 It should be noted that bats of *S. kuhlii* and *S. heathii* found either in sympatry or
688 allopatry do not overlap in most morphological traits (i.e. FA; Figures 3-6). As discussed
689 above, it is very likely that *S. kuhlii* and *S. heathii* have co-existed for a long time. Both
690 species are also known to share similar eco-ethological preferences and feeding guilds (Bates
691 & Harrison, 1997; Francis, 2008; Norberg & Rayner, 1987). Because prey density usually
692 decreases from cluttered to open habitats, strong interspecific competition likely occurred in
693 areas of sympatry during their evolutionary history (Grether et al., 2013; Müller et al., 2012;
694 Roeleke, Johannsen, & Voigt, 2018). To reduce niche overlap, co-existing related species
695 typically evolve mechanisms for resource partitioning (Chevin et al., 2010; Lande, 2014;
696 Tienderen, 1997) that result in detectable differences in morphology or echolocation call

697 parameters (Kingston et al., 2001; Zhang et al., 2007). This would be consistent with the
698 morphological differences between the two species.

699

700 **Acknowledgements**

701

702 We would like to thank numerous agencies and individuals for their research permits and
703 assistance during our study: In Vietnam, the Vietnam Administration of Forestry (MONRE),
704 Nguyen Van Sinh, Le Xuan Canh and Nguyen Quang Truong of the IEBR (Hanoi); in
705 Cambodia, the Centre for Biodiversity Conservation at the Royal University of Phnom Penh
706 and Fauna & Flora International; in Myanmar, the Ministry of Livestock, Fisheries and Rural
707 Development; in Philippines, Juan Carlos T. Gonzalez and Edison A. Cosico of UPLB MNH.
708 We are also grateful to Victor van Cakenberghe (UA, Belgium), Lincoln H. Schmitt (UWA,
709 Australia), and Ibnu Maryanto (LIPI, Indonesia) for their kind help. We also thank the three
710 anonymous reviewers for their helpful comments on the manuscript. This research was
711 supported by the “ATM Barcode” funded by the MNHN, the network “Bibliothèque du
712 Vivant” funded by the CNRS, the MNHN, the INRA, the CEA (Genoscope) to A.H and V.T.T;
713 the Hungarian Scientific Research Fund – OTKA K112440, the National Research,
714 Development and Innovation Fund of Hungary – NKFIH KH130360, and the SYNTHESYS
715 Project, financed by the European Community Research Infrastructure Action under the FP7
716 "Capacities" Program to TG and GC; the NTP-NFTÖ-17 project funded by the Hungarian
717 Ministry of Human Capacities to TG; a grant-in-aid on Research Program on Emerging and
718 Re-emerging Infectious Diseases, Japan Agency for Medical Research and Development
719 (AMED) (JP15fk0108005, JP16fk0108117, JP17fk0108217, JP18fk0108017,
720 JP19fk0108097, and JP20fk0108097), a grant-in-aid from the Japan Society for the
721 Promotion of Science 24405045 to S.A, K.K., and D.F.; the KAKENHI (18H04816,
722 18H02492, 18K19359, 18KK0207) and JRPs-LEAD with DFG to D.K.; the project
723 TN18/T07 funded by the Vietnam Academy of Science and Technology (VAST) to T.A.T and
724 N.T.S.; and the Rufford Foundation (UK).

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726 **Data Availability Statement**

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728 The authors confirm that the data supporting the findings of this study are available within the
729 article and/or its supplementary materials.

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732 **References**

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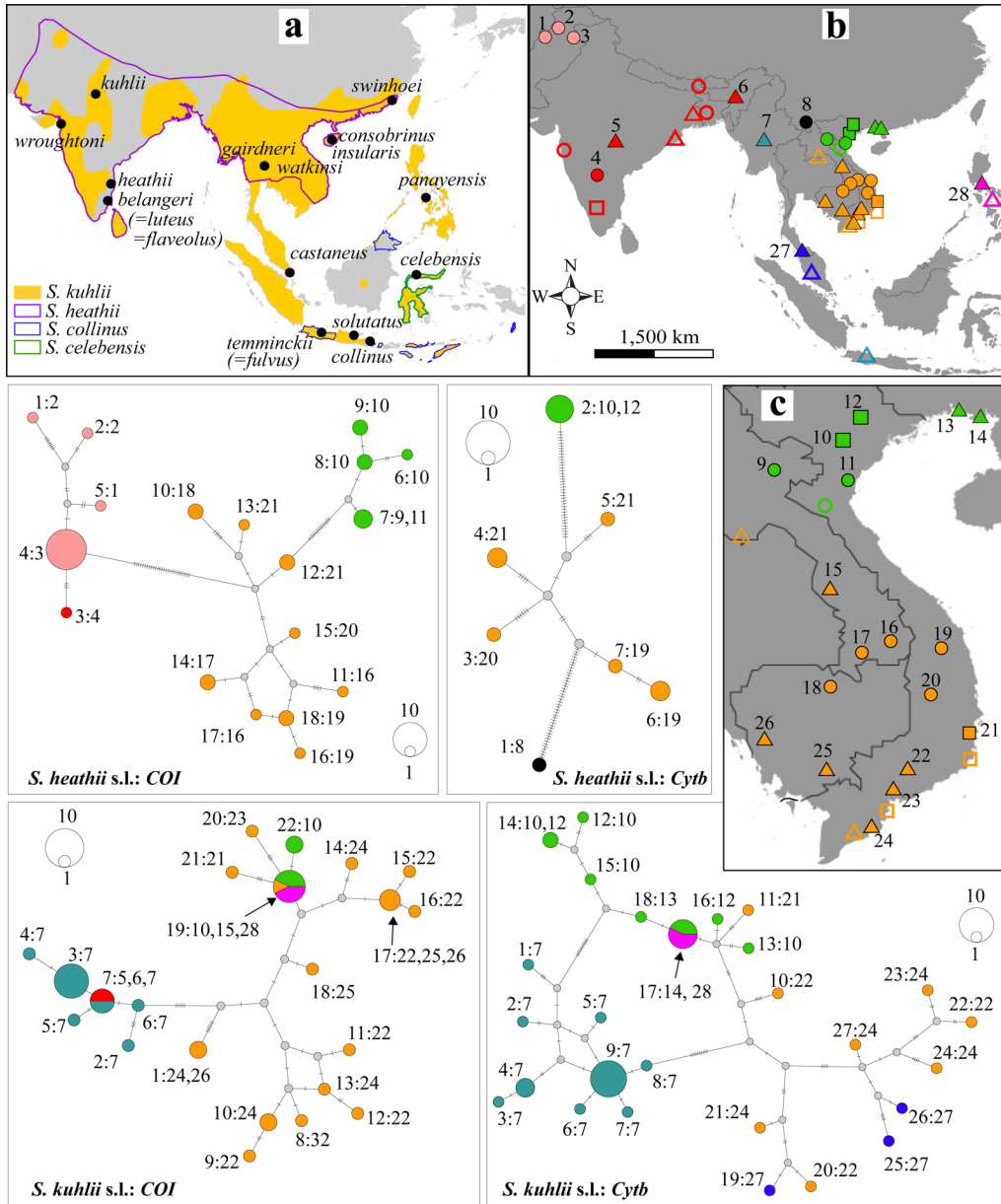
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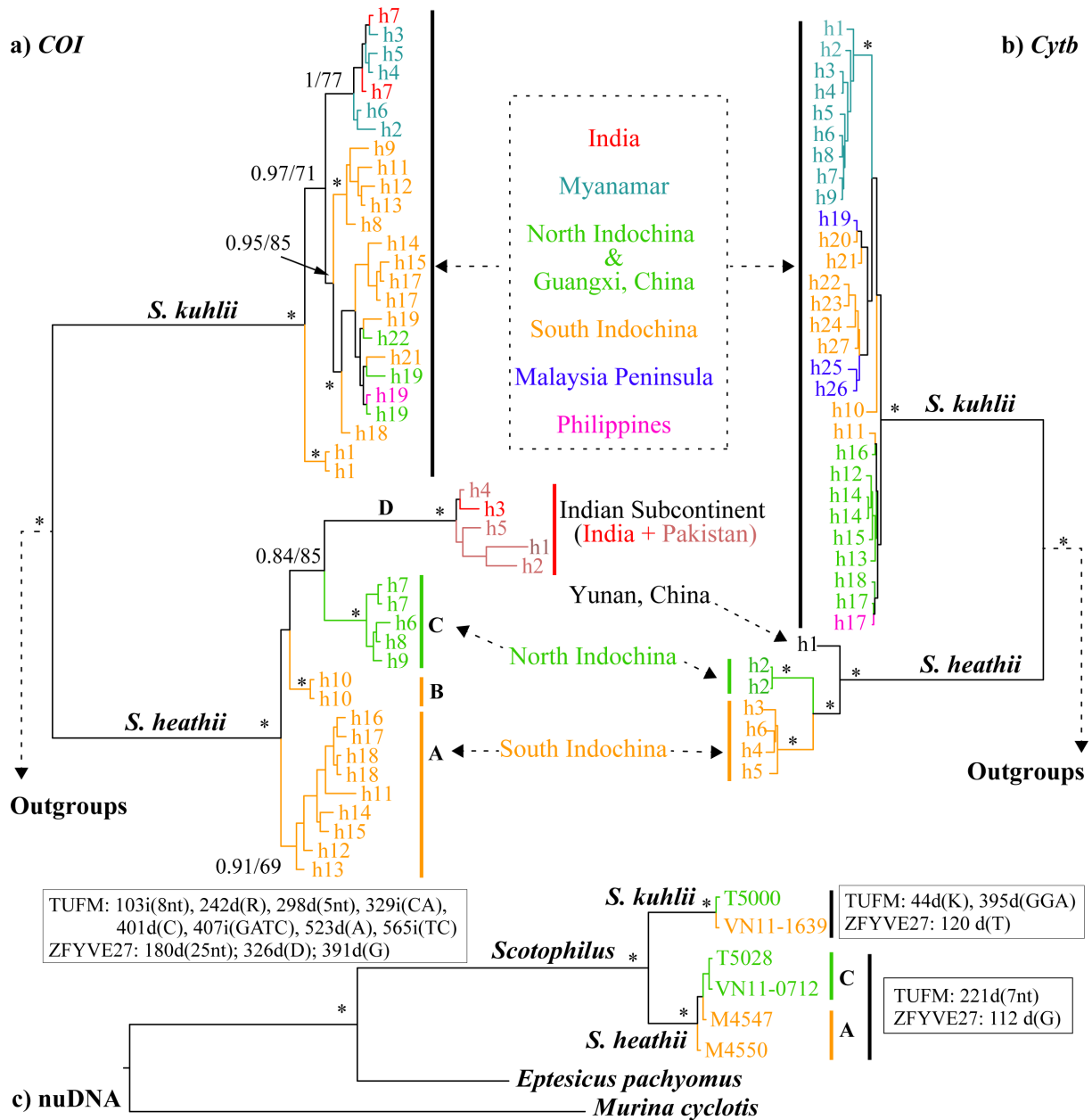
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1040 **Figure 1. Phylogeographic patterns of Asian *Scotophilus* spp. based on the**
 1041 **mitochondrial (*COI* and *Cytb*) markers.**

1042 a: IUCN distribution range of four recently recognized Asian *Scotophilus* spp. Black dots
 1043 refer to type localities of formerly described species or subspecies of *Scotophilus* in Asia (See
 1044 Table S1). Note that the type locality of *S. kuhlii* in India is uncertain. b–c: Locations for
 1045 which specimens of *S. kuhlii*, *S. heathii* or both species were collected are shown as triangles,
 1046 circles and squares, respectively. Localities for specimens included in genetic analyses are
 1047 filled and numbered whereas those of individuals in morphological analyses only are empty.
 1048 MtDNA haplotypes of examined specimens in the TCS networks and their corresponding
 1049 locations are indicated by the same colour and by numbers before and after colons,
 1050 respectively (See Appendix 1 and Table S2 for more details).



1052

1053 **Figure 2. Phylogenetic trees of Asian *Scotophilus* spp. and outgroups.**

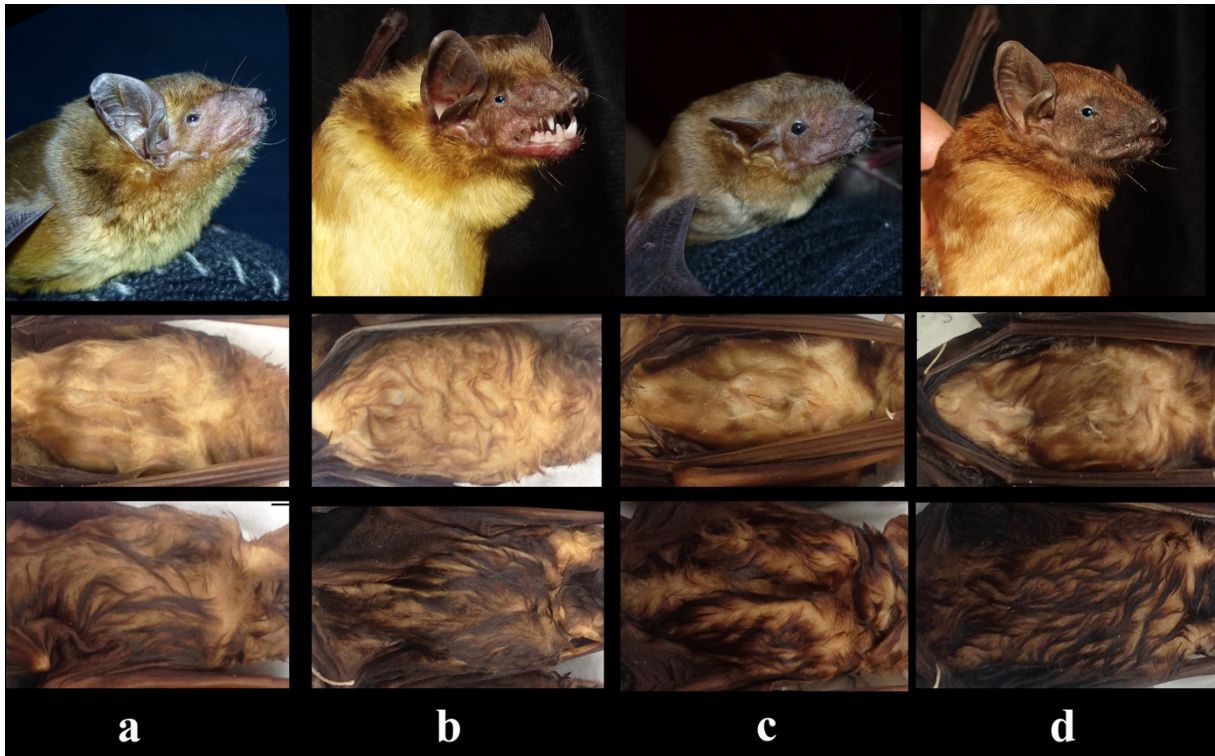
1054 Values on nodes indicate Bayesian posterior probabilities (PP)/Maximum-Likelihood

1055 bootstrap percentage (BP) (PP<0.7 and BP <70% are not shown). The asterisks (*) indicate

1056 that the node was supported by PP≥0.9/BP≥90. The colours of mtDNA haplotypes match

1057 those in Figure 1. The position and nature of all diagnostic indels (i: insertion; d: deletion)

1058 shared by at least two taxa in the alignments of nuclear genes are indicated in boxes.



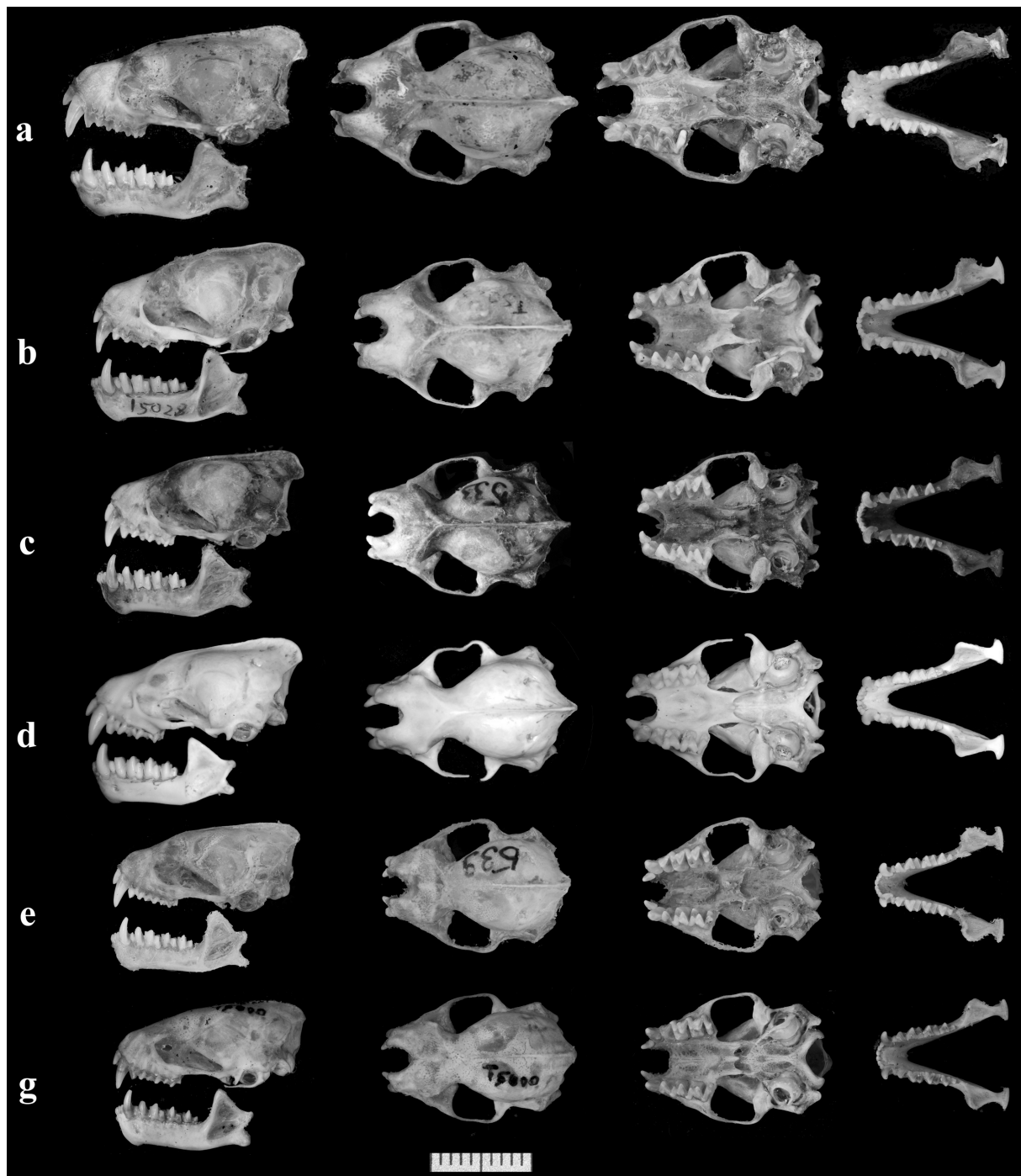
1059

1060 **Figure 3. Live and wet specimens (not to scale) of *Scotophilus heathii* and *S. kuhlii***

1061 **collected in sympatry in two different regions of Vietnam.**

1062 Northern Vietnam (Location 10): a – *S. heathii* / c – *S. kuhlii*. South-Central Vietnam

1063 (Location 21): b – *S. heathii* / d – *S. kuhlii*



1064

1065 **Figure 4. Skull profiles of selected Asian *Scotophilus* spp.**

1066 *S. heathii* s.s.: a – Highland Central Vietnam (loc. 19; IEBR-M-4550), b – Northern Vietnam

1067 (loc. 10; IEBR. T5028) and c – South Central Vietnam (loc. 21; IEBR. VN17-533); *S. ?*

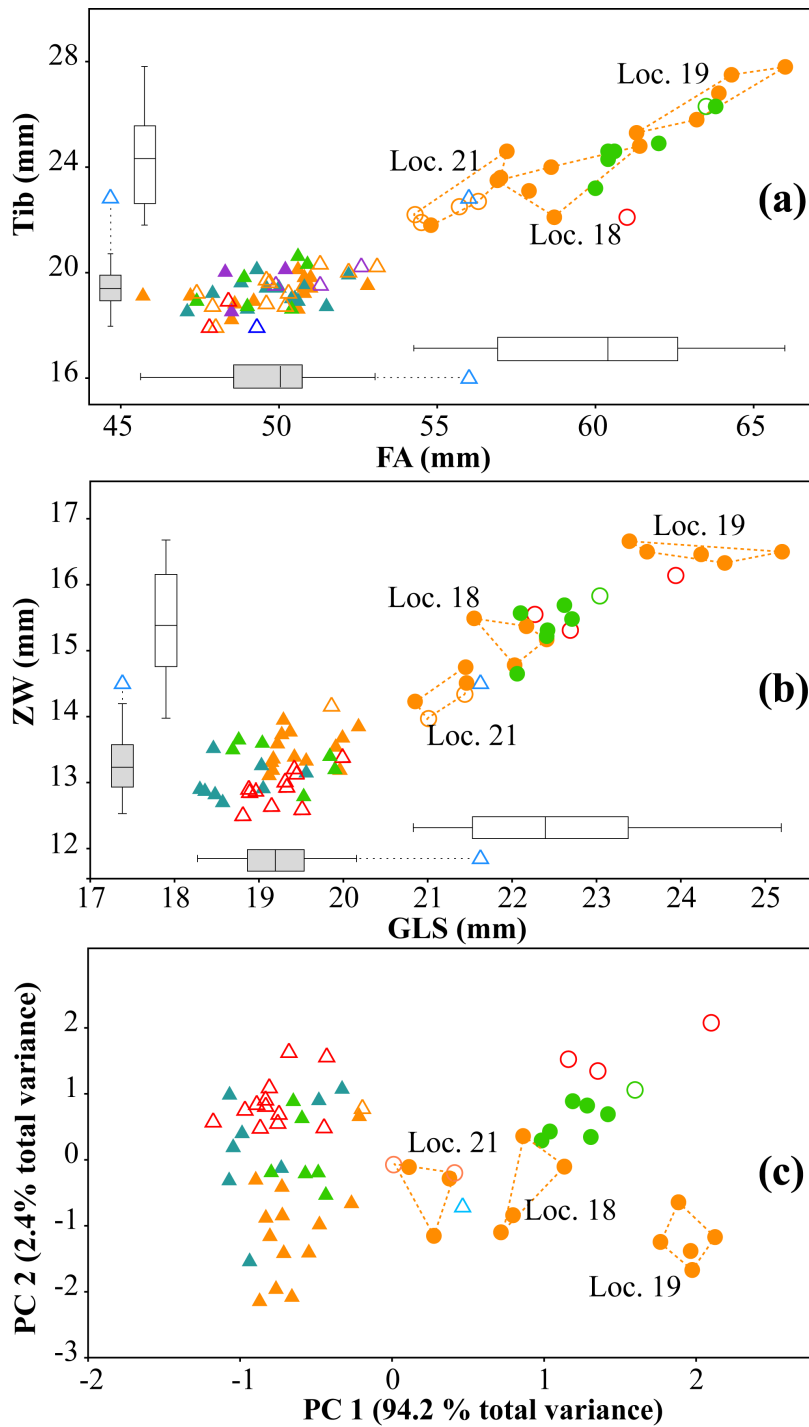
1068 *solutatus* s.s.: d – Java, Indonesia (HNHM 2869.22); and *S. kuhlii* s.s.: e – South Central

1069 Vietnam (loc. 21; IEBR. VN17-539) and g – Northern Vietnam (loc. 10; IEBR. T5000). Scale

1070 =10 mm.

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1073

1074 **Figure 5. Scatter plots from morphological analyses of Asian *Scotophilus* spp.**

1075 a and b: Variation in external (FA vs. Tib) and skull traits (GSL vs. ZB) among specimens of
 1076 *Scotophilus* spp., respectively. Boxplots (with an interquartile range) to find outliers in the

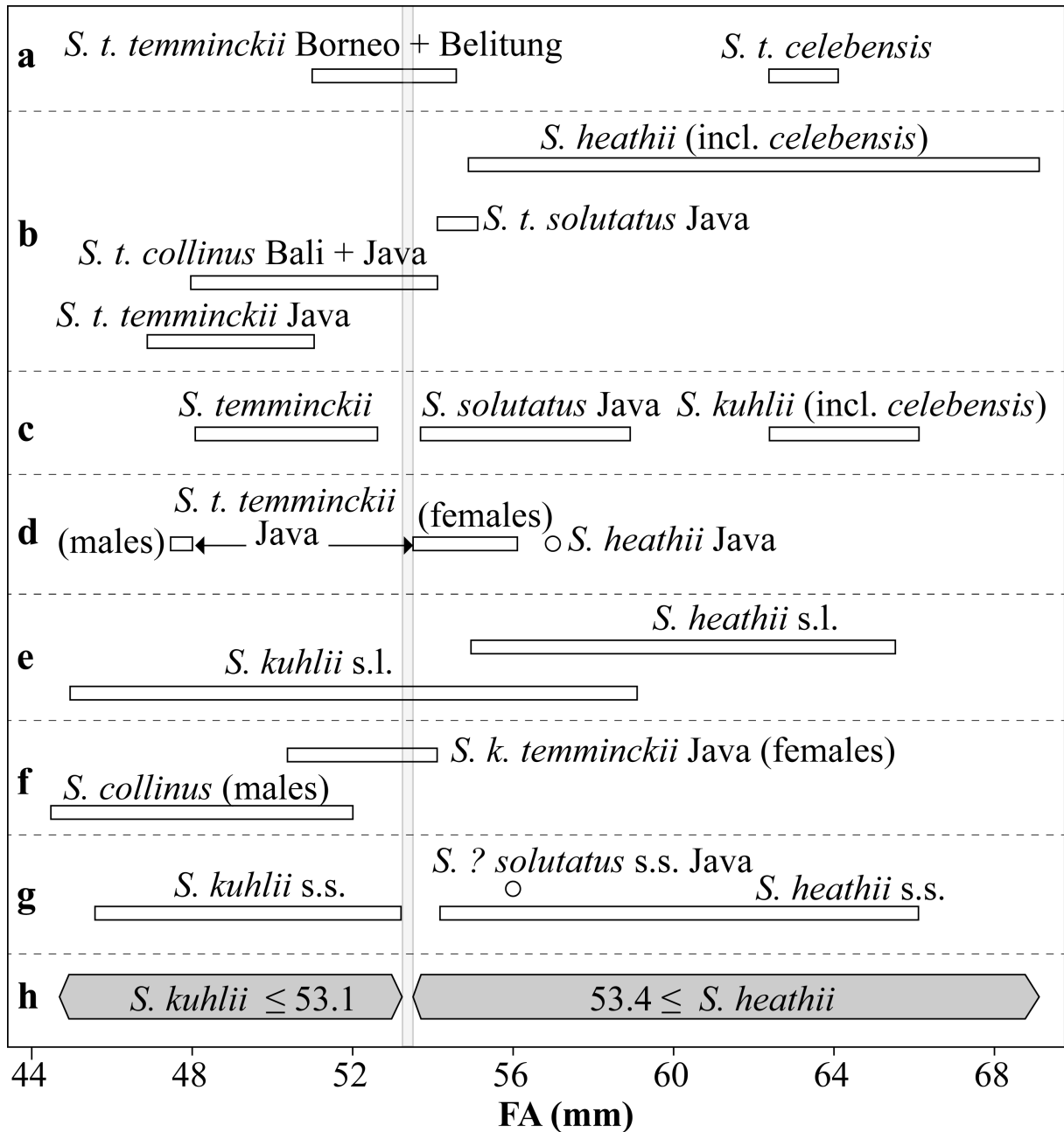
1077 datasets were embedded; c: Plot of PC 1 against PC 2 from PCA on log-transformed

1078 craniodental measurements. The legends of symbols follow Figure 1. Bats of *S. heathii* found

1079 in three spatially isolated locations (18, 19, and 21) in Southern Indochina (Figure 1) appear

1080 as three relatively separated subpopulations.

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1083

Figure 6. Pairwise comparison of FA ranges (min-max) for Asian *Scotophilus* spp.

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recognized in present and previous studies.

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a – Sody, 1928; b – Tate, 1942; c – Shamel, 1942; d – Siddiqi, 1960; e – Corbet & Hill, 1992;

1086

f – Kitchener et al. (1997); g – this study; and h – desired ranges for *S. kuhlii* and *S. heathii*.

1087

1089 Table 1: Synopsis of taxonomic studies on Asian *Scotophilus* between 1940–2000^(†).

Author	Reference materials	Taxonomic treatment
[1]	India, Hainan, Taiwan (Formosa), Malacca, Java, Bali, Luzon	<i>S. kuhlii</i> (forearm length (FA, in mm): 41, immature holotype) <i>S. temminckii</i> (=fulvus) (FA ≤ 51) includes <i>consobrinus</i> , <i>castaneus</i> , <i>wroughtoni</i> , <i>panayensis</i> , <i>collinus</i> , and <i>gairdneri</i> as similar sized races/synonyms and a larger sized Javanese one, <i>solutatus</i> (FA: 55-55).
	India: Kashmir, Myanmar (Burma), Hainan, Sri Lanka (Ceylon)	<i>S. heathii</i> (FA ≥ 54) with <i>belangeri</i> (=luteus=flaveolus), <i>insularis</i> , and <i>celebensis</i> as races/synonyms
[2]	Java, Singapore, Thailand, French Indochina	<i>Pachyotis temminckii</i> (FA: 48.2-52.5) includes <i>temminckii</i> = <i>castaneus</i> , <i>consobrinus</i> , <i>wroughtoni</i> , <i>panayensis</i> , <i>collinus</i> , and <i>gairdneri</i> as synonyms/ races
	West Java, Depok, Pelabuhan	<i>P. solutatus</i> (FA: 53.8-58.9)
	Thailand (Siam), French Indochina, Ceylon	<i>Pachyotis kuhlii</i> (FA: 60-66) includes <i>insularis</i> , and <i>celebensis</i> as races
[3]	Thailand	<i>S. s. solutatus</i> : Java, and <i>S. solutatus watkinsi</i> ssp. nov. (FA: 55.5-60.5). Type locality: Pak Nam Pho, Nakhon Sawan, Thailand.
[4]	Collection in the British Museum (N.H.)	<i>S. t. temminckii</i> (FA of males / females: 47.6-47.9 / 53.4-56.0): Java
		<i>S. t. castaneus</i> (FA: 47.6-52.4): Malay Peninsula; Upper Burma; South China; India: Calcutta
		<i>S. t. wroughtoni</i> (FA: 45.2-52.4): Ceylon and India
		<i>S. h. heathii</i> (56.2-63.8): Ceylon, India, Pakistan, Burma, Siam and Java
[5]	Collection in the British Museum (N.H.)	<i>S. kuhlii</i> replaced <i>S. temminckii</i> as generic name of smaller sized species. Its subspecies/ races include <i>temminckii</i> , <i>castaneus</i> , <i>collinus</i> , <i>consobrinus</i> , <i>gairdneri</i> , <i>panayensis</i> , <i>solutatus</i> and <i>wroughtoni</i> .
		<i>S. h. heathii</i> (Indian and Burma) and <i>S. h. (?) watkinsi</i> (FA: 61.2-61.4)
[6]	Synthesis from previous studies	<i>S. kuhlii</i> (FA: 45-59) comprises <i>castaneus</i> , <i>consobrinus</i> , <i>fulvus</i> , <i>gairdneri</i> , <i>panayensis</i> , <i>solutatus</i> , <i>swinhoi</i> , <i>temminckii</i> , and <i>wroughtoni</i> as synonyms/races found throughout the Indomalayan Region. The largest specimens (or <i>S. k. solutatus</i>) occur apparently in Java.
		<i>S. heathii</i> (FA: 55-65.5) includes <i>belangeri</i> , <i>flaveolus</i> , <i>insularis</i> , <i>luteus</i> , <i>watkinsi</i> (from Afghanistan to Vietnam) and probably <i>celebensis</i> (Sulawesi) as subspecies/synonyms
[7]	<i>S. kuhlii</i> s. l. (FA < 54) collected from Greater (Java), Lesser Sunda and Borneo islands	- <i>S. k. temminckii</i> (FA of males: 52.2-53.7): Java and <i>S. k. solutatus</i> (FA of males: 50.3-52.4): East Java and Bali; - <i>S. collinus</i> : Sundaic form (FA of males: 45.2-51.4): Sabah, Java and Bali; Nusa Tenggara form (FA of males: 44.6-51.9): Lombok to Timor

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1092 ^(†)Prior to the mid-20th century, Asian *Scotophilus* included 17 taxa (species and subspecies)
1093 described as new to science (detailed in Figure 1; Table S1). Authors: 1 – Tate, 1942; 2 –
1094 Shamel, 1942; 3 – Sanborn, 1952; 4 – Siddiqui, 1960; 5 – Hill & Thonglongya, 1972; 6 –
1095 Corbet & Hill, 1992; 7 – Kitchener et al., 1997

1096

1097 **Table 2: Range (min–max) of uncorrected p-distances (%) between Asian *Scotophilus***
 1098 **spp. and selected outgroups, based on *COI* (*Cytb*) (below the diagonal) and nuDNA**
 1099 **(above the diagonal) datasets.**

Taxon		1	2	3	4			
					A	B	C	D
1. <i>M. cyclotis</i>			9.5	11.3-11.7	11.3-11.3	NA	11.6-11.6	NA
2. <i>E. pachyomus</i>		20.1 (19.6)		6.8-7.0	6.8-6.9	NA	6.8-6.9	NA
3. <i>S. kuhlii</i>		21.1 -22.7 (19.7-20.3)	20.9-21.8 (21.1-21.7)	0.0 2.3(2.2)	1.4-1.6	NA	1.5-1.7	NA
4. <i>S. heathii</i>	A	21.5-22.1 (22.1-22.5)	20.5-21.2 (21.1-21.3)	13.9-15.2 (14.5-15.9)	0.0 1.6 (1.0)	NA	0.0-0.1	NA
	B	21.8-21.8 (NA)	21.3-21.3 (NA)	14.3-15.4 (NA)	1.1-2.3 (NA)	NA 0.0 (NA)	NA	NA
	C	21.8-22.1 (21.8-21.8)	21.0 - 21.2 (20.6-20.6)	14.3 - 15.7 (15.2-16.0)	2.6-4.0 (3.7-3.9)	NA (3.8-4.2)	0.0 0.6 (0-0)	NA
	D	21.9-23.4 (NA)	20.7 -21.3 (NA)	16.0-18.3 (NA)	5.2-7.6 (NA)	5.5-6.9 (NA)	5.1-7.1 (NA)	NA 2.0 (NA)
	E	NA (21.4)	NA (21.1)	NA (14.0-14.9)	NA (4.0-4.0)	NA (NA)	NA (3.8-4.2)	NA (NA)

1100
 1101 Taxon: A – D and E are corresponding lineages A – D and Yunnan, China of *S. heathii* in
 1102 Figure 2. Values in diagonal in bold show the maximum intraspecific distances within each
 1103 taxon calculated from the respective datasets; NA – not available.

1104

1105 **Table 3: External and craniodental measurements (in mm) of Asian *Scotophilus* spp.** Values are given as mean \pm SD, n; min–max.

1106 Acronyms and definitions for measurements are given in the Materials and Methods section.

Character	<i>S. kuhlii</i> s.l.							<i>S. heathii</i> s.l.		
	North Indochina	South Indochina	Myanmar	Indian Subcontinental	Malaysia Peninsula	Philippines	Indonesia (Java)*	North Indochina	South Indochina	Indian Subcontinental
FA	49.5 \pm 1.3; 6 47.4 – 50.9	49.9 \pm 1.7; 26 45.7 – 53.1	49.8 \pm 1.4; 14 47.1 – 52.2	48.1 \pm 0.4; 2 47.8 – 48.4	49.3; 1	50.1 \pm 1.6; 6 48.3 – 52.6	56.0; 1	61.5 \pm 1.6; 7 60.0 – 63.8	58.9 \pm 3.7; 17 54.3 – 66.0	61.0; 1
Tib	19.6 \pm 0.9; 6 18.7 – 20.7	19.4 \pm 0.6; 26 18.0 – 20.4	19.3 \pm 0.5; 14 18.6 – 20.2	18.5 \pm 0.8; 2 18.0 – 19.0	18.0; 1	19.7 \pm 0.6; 6 18.6 – 20.3	22.9; 1	24.9 \pm 1.1; 7 23.2 – 26.3	24.1 \pm 2.0; 17 21.8 – 27.8	22.1; 1
GSL	19.29 \pm 0.54; 6 18.69 – 19.90	19.54 \pm 0.37; 14 19.15 – 20.18	18.73 \pm 0.44; 8 18.30 – 19.56	19.24 \pm 0.34; 12 18.81 – 19.99	–	–	21.68; 1	22.48 \pm 0.35; 7 22.06 – 23.04	22.52 \pm 1.41; 14 20.85 – 25.20	22.97 \pm 0.87; 3 22.27 – 23.94
SL	18.45 \pm 0.52; 6 17.66 – 19.11	18.70 \pm 0.27; 14 18.19 – 19.11	18.25 \pm 0.51; 8 17.64 – 18.98	18.17 \pm 0.33; 12 17.68 – 18.80	–	–	20.43; 1	21.37 \pm 0.35; 7 20.80 – 21.90	21.43 \pm 1.34; 14 19.78 – 23.50	21.83 \pm 0.96; 3 20.97 – 22.87
CBL	17.59 \pm 0.25; 6 17.30 – 17.90	17.49 \pm 0.30; 14 16.95 – 17.90	17.30 \pm 0.58; 8 16.48 – 18.05	17.10 \pm 0.33; 12 16.40 – 17.61	–	–	18.76; 1	19.76 \pm 0.33; 7 19.31 – 20.26	19.74 \pm 1.26; 14 17.97 – 21.39	20.00 \pm 0.76; 3 19.32 – 20.82
CCL	17.55 \pm 0.19; 6 17.24 – 17.81	17.71 \pm 0.30; 14 17.27 – 18.21	17.34 \pm 0.53; 8 16.80 – 18.11	17.44 \pm 0.28; 12 16.93 – 17.83	–	–	19.26; 1	20.01 \pm 0.42; 7 19.46 – 20.48	19.94 \pm 1.30; 14 18.14 – 21.61	20.47 \pm 0.85; 3 19.72 – 21.40
ZB	13.39 \pm 0.32; 6 12.82 – 13.68	13.61 \pm 0.30; 14 13.22 – 14.19	13.05 \pm 0.27; 8 12.73 – 13.55	12.96 \pm 0.26; 12 12.53 – 13.41	–	–	14.54; 1	15.39 \pm 0.39; 7 14.65 – 15.83	15.36 \pm 0.97; 14 13.97 – 16.66	15.67 \pm 0.43; 3 15.31 – 16.14
C¹C¹	6.26 \pm 0.10; 6 6.10 – 6.35	6.14 \pm 0.24; 14 5.75 – 6.58	6.23 \pm 0.27; 8 5.95 – 6.66	6.39 \pm 0.17; 12 6.11 – 6.68	–	–	6.69; 1	7.39 \pm 0.22; 7 7.04 – 7.77	7.08 \pm 0.33; 14 6.63 – 7.63	7.89 \pm 0.43; 3 7.56 – 8.38
M³M³	8.72 \pm 0.22; 6 8.36 – 9.03	8.45 \pm 0.26; 14 7.95 – 8.89	8.32 \pm 0.21; 8 8.00 – 8.63	8.39 \pm 0.14; 12 8.11 – 8.63	–	–	8.95; 1	9.72 \pm 0.28; 7 9.29 – 10.12	9.51 \pm 0.49; 14 8.79 – 10.36	9.81 \pm 0.31; 3 9.63 – 10.16
CM³	6.62 \pm 0.09; 6 6.49 – 6.77	6.52 \pm 0.19; 14 6.35 – 6.99	6.52 \pm 0.14; 8 6.34 – 6.75	6.58 \pm 0.16; 12 6.30 – 6.84	–	–	7.26; 1	7.55 \pm 0.13; 7 7.32 – 7.68	7.26 \pm 0.44; 14 6.72 – 7.94	7.74 \pm 0.23; 3 7.59 – 8.00
ML	13.69 \pm 0.13; 6 13.49 – 13.82	13.75 \pm 0.22; 14 13.41 – 14.13	13.72 \pm 0.26; 8 13.32 – 14.10	13.41 \pm 0.24; 12 13.09 – 13.90	–	–	14.89; 1	15.86 \pm 0.32; 7 15.34 – 16.24	15.51 \pm 1.05; 15 14.14 – 17.00	15.81 \pm 0.62; 3 15.25 – 16.47
CM₃	7.53 \pm 0.17; 6 7.30 – 7.80	7.42 \pm 0.21; 14 7.09 – 7.88	7.36 \pm 0.17; 8 7.12 – 7.67	7.36 \pm 0.11; 12 7.20 – 7.56	–	–	7.92; 1	8.65 \pm 0.20; 7 8.37 – 8.89	8.28 \pm 0.47; 15 7.63 – 8.96	8.79 \pm 0.33; 3 8.57 – 9.17

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* – This specimen resembles *S. ? solutatus* (Shamel, 1942; Tate, 1942)

1109 **Appendix 1. Asian *Scotophilus* specimens were collected and/or examined directly by the authors in this study.**

1110 See Material and Methods for acronyms of museums and genetic markers. (†) – tissue samples only. (‡) – Localities for specimens included in
 1111 molecular analyses are indicated by numbers (after colon) as shown in Figure 1. Country codes include: IN – India, KH – Cambodia; LA – Laos;
 1112 and VN – Vietnam. (§) – Numbers (in parentheses) after Genbank accession numbers for *Cytb* and *COI* sequences of *Scotophilus* specimens are
 1113 respective haplotypes shown in Figure 1 and 2.

Taxon	Museum/Sample code	Location(‡)	Genbank Accession No.			
			<i>Cytb</i> (§)	<i>COI</i> (§)	<i>TUFM</i>	<i>ZFYVE27</i>
<i>S. heathii</i> (♂)	HNHM 65.23.1.	Bharatpur, Rajasthan, IN	–	–	–	–
<i>S. heathii</i> (♀)	HNHM 92.120.1. (11951)	Elephanta caves, Mumbai, Maharashtra, IN	–	–	–	–
<i>S. heathii</i> (♂)	HNHM 93.36.1. (12175)	Coimbatore, Tamil Nadu, IN	–	–	–	–
<i>S. heathii</i> (♂)	HNHM 93.37.1. (12207)	Sevoke, IN	–	–	–	–
<i>S. heathii</i> (♂)	HNHM 92.119.1. (11526)	N.Salt Lake, Nalbani, BD	–	–	–	–
<i>S. heathii</i> (♂)	IEBR.Tu.04.09.09.1 (T5028)	Xom Hau, Dong Anh, Hanoi, VN: 10	–	MT821518 (6)	–	–
<i>S. heathii</i> (♀)	IEBR.Tu.10.08.09.1 (T5029)	Ho Tay, Tay Ho, Ha Noi, VN: 10	–	MT821519 (8)	–	–
<i>S. heathii</i> (♀)	IEBR.VN15-47 (VN6149)	Xom Hau, Dong Anh, Hanoi, VN: 10	MT820603 (2)	MT821506 (9)	–	–
<i>S. heathii</i> (♂)	IEBR.VN15-49 (VN6151)	Xom Hau, Dong Anh, Hanoi, VN: 10	MT820604 (2)	MT821505 (9)	–	–
<i>S. heathii</i> (♀)	IEBR.VN15-50 (VN6152)	Xom Hau, Dong Anh, Hanoi, VN: 10	MT820605 (2)	MT821504 (8)	–	–
<i>S. heathii</i> (♀)	IEBR.VN11-0712	Ngoc Lac, Thanh Hoa, VN: 11	–	MT821517 (7)	–	–
<i>S. heathii</i> (♀)	IEBR.PH24 (VN7297)	Pu Huong, Nghe An, VN	–	–	–	–
<i>S. heathii</i> (♂)	CBC01250 (VN11-1648)	Preah Vihear protected forest, KH: 18	–	MT821520 (10)	–	–
<i>S. heathii</i> (♀)	CBC01251	Preah Vihear protected forest, KH: 18	–	–	–	–
<i>S. heathii</i> (♀)	CBC01252 (VN11-1649)	Preah Vihear protected forest, KH: 18	–	MT821521(10)	–	–
<i>S. heathii</i> (♀)	CBC01260	Preah Vihear protected forest, KH: 18	–	–	–	–
<i>S. heathii</i> (♂)	HNHM 2014.11.26 (23702)	Preah Vihear protected forest, KH	–	–	–	–

Taxon	Museum/Sample code	Location ^(*)	Genbank Accession No.			
			<i>Cytb</i> ^(§)	<i>COI</i> ^(§)	<i>TUFM</i>	<i>ZFYVE27</i>
<i>S. heathii</i> (♀)	IEBR.M4547	Ba To, Quang Ngai, VN: 19	–	–	–	–
<i>S. heathii</i> (♀)	IEBR.M4548	Ba To, Quang Ngai, VN: 19	–	–	–	–
<i>S. heathii</i> (♂)	IEBR.M4550 (VN7293)	Ba To, Quang Ngai, VN: 19	–	–	–	–
<i>S. heathii</i> (♂)	IEBR.M4553 (VN1736/VN7294)	Ba To, Quang Ngai, VN: 19	MT820609 (6)	MT821522 (18)	MT820615	MT820621
<i>S. heathii</i> (♀)	IEBR.M4554 (VN7295)	Ba To, Quang Ngai, VN: 19	MT820611 (7)	MT821507 (16)		
<i>S. heathii</i> (♂)	IEBR.M4555 (VN1737/VN7296)	Ba To, Quang Ngai, VN: 19	MT820610 (6)	MT821523 (18)	MT820616	MT820622
<i>S. heathii</i> (♀)	IEBR.VN17-532 (VN7299)	Loi Hai, Ninh Thuan, VN: 21	MT820606 (3)	MT821509 (12)	–	–
<i>S. heathii</i> (♂)	IEBR.VN17-533 (VN7300)	Loi Hai, Ninh Thuan, VN: 21	MT820607 (3)	MT821510 (12)	–	–
<i>S. heathii</i> (♀)	IEBR.VN17-536 (VN7302)	Loi Hai, Ninh Thuan, VN: 21	MT820608 (5)	MT821508 (13)	–	–
<i>S. heathii</i> (♀)	IEBR.VN17-537	Lien Huong, Binh Thuan, VN	–	–	–	–
<i>S. heathii</i> (♂)	IEBR.VN17-538 (VN7303)	Lien Huong, Binh Thuan, VN	–	–	–	–
<i>S. heathii</i> (?)	IEBR.Tu.18.5.17.2	Lien Huong, Binh Thuan, VN	–	–	–	–
<i>S. heathii</i> (♂)	IEBR.Tu.18.5.17.3	Lien Huong, Binh Thuan, VN	–	–	–	–
<i>S. kuhlii</i> (♂)	HNHM 92.121.1. (11548)	Calcutta, West Bengal, IN	–	–	–	–
<i>S. kuhlii</i> (♂)	HNHM 92.123.1. (11600)	Calcutta, West Bengal, IN	–	–	–	–
<i>S. kuhlii</i> (♂)	HNHM 92.123.2. (11601)	Calcutta, West Bengal, IN	–	–	–	–
<i>S. kuhlii</i> (♂)	HNHM 92.123.3. (11602)	Calcutta, West Bengal, IN	–	–	–	–
<i>S. kuhlii</i> (♂)	HNHM 92.123.4. (11603)	Calcutta, West Bengal, IN	–	–	–	–
<i>S. kuhlii</i> (♂)	HNHM 92.123.5. (11604)	Calcutta, West Bengal, IN	–	–	–	–
<i>S. kuhlii</i> (♂)	HNHM 92.123.6. (11605)	Calcutta, West Bengal, IN	–	–	–	–
<i>S. kuhlii</i> (♂)	HNHM 92.155.1. (11606)	Calcutta, West Bengal, IN	–	–	–	–
<i>S. kuhlii</i> (♂)	HNHM 92.123.7. (11608)	Calcutta, West Bengal, IN	–	–	–	–
<i>S. kuhlii</i> (♂)	HNHM 92.123.8. (11609)	Calcutta, West Bengal, IN	–	–	–	–

Taxon	Museum/Sample code	Location ^(*)	Genbank Accession No.			
			<i>Cytb</i> ^(§)	<i>COI</i> ^(§)	<i>TUFM</i>	<i>ZFYVE27</i>
<i>S. kuhlii</i> (♂)	HNHM 93.34.1. (12100)	Ganespur, West Bengal, IN	–	–	–	–
<i>S. kuhlii</i> (♀)	HNHM 93.35.1. (12176)	Mettupalayam, Tamil Nadu, IN	–	–	–	–
<i>S. kuhlii</i> (♂)	HNHM 92.122.1. (11565)	Ruined Hindu temple, Konarka, Orissa, IN	–	–	–	–
<i>S. kuhlii</i> (♂)	MM3297 ^(†)	Nay Pyi Daw, Myanmar: 7	MT820592 (9)	–	–	–
<i>S. kuhlii</i> (♂)	MM3298 ^(†)	Nay Pyi Daw, Myanmar: 7	MT820576 (3)	–	–	–
<i>S. kuhlii</i> (♀)	MM3300 ^(†)	Nay Pyi Daw, Myanmar: 7	MT820593 (9)	–	–	–
<i>S. kuhlii</i> (♀)	MM3301 ^(†)	Nay Pyi Daw, Myanmar: 7	MT820577 (4)	–	–	–
<i>S. kuhlii</i> (♀)	MM3302 ^(†)	Nay Pyi Daw, Myanmar: 7	MT820583 (8)	–	–	–
<i>S. kuhlii</i> (♀)	MM3303 ^(†)	Nay Pyi Daw, Myanmar: 7	MT820594 (9)	–	–	–
<i>S. kuhlii</i> (♂)	MM3304 ^(†)	Nay Pyi Daw, Myanmar: 7	MT820578 (1)	–	–	–
<i>S. kuhlii</i> (♀)	MM3305 ^(†)	Nay Pyi Daw, Myanmar: 7	MT820579 (1)	–	–	–
<i>S. kuhlii</i> (♀)	UTHF.MM3168B1	Nay Pyi Daw, Myanmar: 7	MT820584 (9)	MT821492 (3)	–	–
<i>S. kuhlii</i> (♂)	UTHF.MM3169B2	Nay Pyi Daw, Myanmar: 7	MT820581 (6)	MT821503 (5)	–	–
<i>S. kuhlii</i> (♂)	UTHF.MM3170B3	Nay Pyi Daw, Myanmar: 7	MT820575 (2)	MT821491 (6)	–	–
<i>S. kuhlii</i> (♂)	UTHF.MM3171B4	Nay Pyi Daw, Myanmar: 7	MT820585 (9)	MT821502 (7)	–	–
<i>S. kuhlii</i> (♀)	UTHF.MM3172B5	Nay Pyi Daw, Myanmar: 7	MT820586 (9)	MT821499 (3)	–	–
<i>S. kuhlii</i> (♀)	UTHF.MM3173B6	Nay Pyi Daw, Myanmar: 7	Unassigned (9)	MT821498 (3)	–	–
<i>S. kuhlii</i> (♀)	UTHF.MM3174B7	Nay Pyi Daw, Myanmar: 7	MT820587 (9)	MT821500 (4)	–	–
<i>S. kuhlii</i> (♀)	UTHF.MM3175B8	Nay Pyi Daw, Myanmar: 7	MT820574 (1)	MT821490 (2)	–	–
<i>S. kuhlii</i> (♀)	UTHF.MM3176B9	Nay Pyi Daw, Myanmar: 7	MT820588 (9)	MT821497 (3)	–	–
<i>S. kuhlii</i> (♀)	UTHF.MM3182B13	Nay Pyi Daw, Myanmar: 7	MT820589 (9)	MT821496 (3)	–	–
<i>S. kuhlii</i> (♀)	UTHF.MM3183B14	Nay Pyi Daw, Myanmar: 7	MT820590 (9)	MT821495 (3)	–	–
<i>S. kuhlii</i> (♀)	UTHF.MM3184B15	Nay Pyi Daw, Myanmar: 7	MT820591 (9)	MT821501 (7)	–	–

Taxon	Museum/Sample code	Location ^(*)	Genbank Accession No.			
			<i>Cytb</i> ^(§)	<i>COI</i> ^(§)	<i>TUFM</i>	<i>ZFYVE27</i>
<i>S. kuhlii</i> (♀)	UTHF.MM3185B16	Nay Pyi Daw, Myanmar: 7	MT820582 (7)	MT821494 (3)	–	–
<i>S. kuhlii</i> (♀)	UTHF.MM3186B17	Nay Pyi Daw, Myanmar: 7	MT820580 (5)	MT821493 (3)	–	–
<i>S. kuhlii</i> (♂)	IEBR.Tu.04.05.10.1 (T5000)	Xom Hau, Dong Anh, Hanoi, VN: 10	–	MT821515 (16)	MT820617	MT820623
<i>S. kuhlii</i> (♂)	IEBR.Tu.04.09.09.3 (T5001)	Xom Hau, Dong Anh, Hanoi, VN: 10	–	MT821516 (16)	–	–
<i>S. kuhlii</i> (♂)	IEBR.VN15-43 (VN6145)	Xom Hau, Dong Anh, Hanoi, VN: 10	MT820599 (15)	MT821486 (16)	–	–
<i>S. kuhlii</i> (♂)	VN15-44 (VN6146) ^(†)	Xom Hau, Dong Anh, Hanoi, VN: 10	MT820597 (13)	MT821488 (15)	–	–
<i>S. kuhlii</i> (♂)	IEBR.VN15-45 (VN6147)	Xom Hau, Dong Anh, Hanoi, VN: 10	MT820596 (12)	MT821489 (15)	–	–
<i>S. kuhlii</i> (♂)	IEBR.VN15-51 (VN6153)	Xom Hau, Dong Anh, Hanoi, VN: 10	MT820598 (14)	MT821487 (16)	–	–
<i>S. kuhlii</i> (♂)	IEBR.VN17-46 (VN7397)	Xom Hau, Dong Anh, Hanoi, VN: 10	–	Unassigned (16)	–	–
<i>S. kuhlii</i> (♂)	HNHM 98.46.1. (16574)	Vientiane, LA	–	–	–	–
<i>S. kuhlii</i> (♀)	IEBR.VN17-355 (VN7298)	Loi Hai, Ninh Thuan, VN: 21	–	–	–	–
<i>S. kuhlii</i> (♀)	IEBR.VN17-534 (VN7301)	Loi Hai, Ninh Thuan, VN: 21	MT820595 (11)	MT821482 (14)	–	–
<i>S. kuhlii</i> (♂)	IEBR.VN17-539 (VN7304)	Lien Huong, Binh Thuan, VN	–	–	–	–
<i>S. kuhlii</i> (?)	IEBR.Tu.18.5.17.1	Lien Huong, Binh Thuan, VN	–	–	–	–
<i>S. kuhlii</i> (♀)	IEBR.VN19-04	Vinh Loi, Bac Lieu, VN	–	–	–	–
<i>S. kuhlii</i> (♀)	IEBR.VN19-05	Vinh Loi, Bac Lieu, VN	–	–	–	–
<i>S. kuhlii</i> (♀)	IEBR.VN19-06	Vinh Loi, Bac Lieu, VN	–	–	–	–
<i>S. kuhlii</i> (♀)	IEBR.VN19-07	Vinh Loi, Bac Lieu, VN	–	–	–	–
<i>S. kuhlii</i> (♀)	IEBR.VN19-08	Vinh Loi, Bac Lieu, VN	–	–	–	–
<i>S. kuhlii</i> (♀)	IEBR.VN19-09	Vinh Loi, Bac Lieu, VN	–	–	–	–
<i>S. kuhlii</i> (♀)	IEBR.VN19-10	Vinh Loi, Bac Lieu, VN	–	–	–	–
<i>S. kuhlii</i> (♀)	IEBR.VN19-11	Vinh Loi, Bac Lieu, VN	–	–	–	–
<i>S. kuhlii</i> (♀)	IEBR.VN19-12	Vinh Loi, Bac Lieu, VN	–	–	–	–

Taxon	Museum/Sample code	Location ^(*)	Genbank Accession No.			
			<i>Cytb</i> ^(§)	<i>COI</i> ^(§)	<i>TUFM</i>	<i>ZFYVE27</i>
<i>S. kuhlii</i> (♀)	IEBR.VN19-13	Vinh Loi, Bac Lieu, VN	–	–	–	–
<i>S. kuhlii</i> (♂)	IEBR.VN19-14	Vinh Loi, Bac Lieu, VN	–	–	–	–
<i>S. kuhlii</i> (♀)	IEBR.VN19-15	Vinh Loi, Bac Lieu, VN	–	–	–	–
<i>S. kuhlii</i> (♂)	CBC01861	Bang Chureng, S'ang, Kandal, KH: 25	–	–	–	–
<i>S. kuhlii</i> (♀)	CBC01862	Bang Chureng, S'ang, Kandal, KH: 25	–	–	–	–
<i>S. kuhlii</i> (♀)	CBC01863	Bang Chureng, S'ang, Kandal, KH: 25	–	–	–	–
<i>S. kuhlii</i> (♀)	CBC01864	Bang Chureng, S'ang, Kandal, KH: 25	–	–	–	–
<i>S. kuhlii</i> (♂)	CBC01865	Bang Chureng, S'ang, Kandal, KH: 25	–	–	–	–
<i>S. kuhlii</i> (♂)	CBC01866 (VN11-1642)	Bang Chureng, S'ang, Kandal, KH: 25	–	MT821512 (12)	–	–
<i>S. kuhlii</i> (♂)	CBC01867 (VN11-1640)	Bang Chureng, S'ang, Kandal, KH: 25	–	MT821513 (11)	–	–
<i>S. kuhlii</i> (♂)	CBC01870 (VN11-1641)	Prey Toch, Moug Russey, Battambang, KH: 26	–	MT821514 (11)	–	–
<i>S. kuhlii</i> (♂)	CBC01871 (VN11-1639)	Prey Toch, Moug Russey, Battambang, KH: 26	–	MT821511 (1)	MT820617	MT820624
<i>S. kuhlii</i> (♂)	HNHM 98.14.27. (15672)	Selangor, Malaysia	–	–	–	–
<i>S. kuhlii</i> (♂)	UPLB-MNH paa1548 (MT1706)	Quezon city, Luzon Island, Philippines: 28	MT820600 (17)	MT821484 (16)	–	–
<i>S. kuhlii</i> (♂)	UPLB-MNH paa1550 (MT1707)	Quezon city, Luzon Island, Philippines: 28	MT820601 (17)	MT821483 (16)	–	–
<i>S. kuhlii</i> (♀)	UPLB-MNH paa1552 (MT1709)	Quezon city, Luzon Island, Philippines: 28	MT820602 (17)	MT821485 (16)	–	–
<i>S. kuhlii</i> (♂)	UPLB-MNH jdva1064 (3873)	Sibuyan Island, Philippines	–	–	–	–
<i>S. kuhlii</i> (♀)	UPLB-MNH jdva1065 (3874)	Sibuyan Island, Philippines	–	–	–	–
<i>S. kuhlii</i> (♀)	UPLB-MNH jdva1066 (3875)	Sibuyan Island, Philippines	–	–	–	–
<i>S. ? solutatus</i>	HNHM 2869.22 (ori. ID: <i>S. kuhlii</i>)	Java, Indonesia	–	–	–	–

SUPPORTING INFORMATION

Integrative taxonomy and biogeography of Asian yellow house bats (Vespertilionidae: *Scotophilus*) in the Indomalayan Region

Vuong Tan Tu, Tamás Görföl, Gábor Csorba, Satoru Arai, Fuka Kikuchi, Dai Fukui, Daisuke Koyabu, Neil M. Furey, Saw Bawm, Kyaw San Lin, Phillip Alviola, Chu Thi Hang, Nguyen Truong Son, Tran Anh Tuan, and Alexandre Hassanin

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Figure S5. Correlation between mean PC1's scores from PCA of skull characters and FA values of Asian *Scotophilus* spp.

*** References cited in the Supporting Information**

Table S1. List of species and subspecies of Asian *Scotophilus* described as new to science prior to the mid-20th century.

No.	Taxa	FA (in mm)	Type locality	Reference
1	<i>S. kuhlii</i>	41 (immature)	?, India	Leach, 1821
2	<i>Vespertilio temminckii</i>	47-51 (small)	Java	Horsfield, 1824
3	<i>Nycticejus heathii</i>	> <i>V. temminckii</i>	Mandas, Continental India	Horsfield, 1831
4	<i>Vespertilio belangeri</i>	55.9	Pondicharry, Coromandel, India	Geoffroy I., 1834
5	<i>Scotophilus fulvus</i>	Unknown	?, Java	Gray, 1843
6	<i>Nycticejus luteus</i>	large	Bengal, Coromandel	Blyth, 1851
7	<i>Nycticejus castaneus</i>	= <i>N. temminckii</i>	Malacca	Horsfield, 1851
8	<i>Nycticejus flaveolus</i>	Large	Continental India	Horsfield, 1851
9	<i>Nycticejus (?) swinhoei</i>	50.8	Amoy (=Xiamen), China	Blyth, 1860
10	<i>Scotophilus wroughtoni</i>	50	Kim (Surat), India	Thomas, 1897
11	<i>Scotophilus castaneus consobrinus</i>	50-52	Hainan Is. China	Allen, 1906
12	<i>S. kuhlii insularis</i>	64-67	Hainan Is. China	Allen, 1906
13	<i>Scotophilus gairdneri</i>	48	Paknampo, Central Siam	Kloss, 1917
14	<i>Pachyotis temminckii panayensis</i>	48	Panay Island, Philippines	Sody, 1928
15	<i>Pachyotis temminckii celebensis</i>	63.5-64	Toli-toli, Celebes	Sody, 1928
16	<i>Scotophilus temminckii collinus</i>	48-54	Bali	Sody, 1936
17	<i>Scotophilus castaneus solutatus</i>	50-56; holotype (55)	Tjandiroto, East Java	Sody, 1936

Table S2. Genetic sequences of Asian *Scotophilus* spp. and outgroups in GenBank included in molecular analyses in the present study.

([†]) –Locations of specimens included in molecular analyses are indicated by numbers (after colon) as representing in Figure 1. Country codes include: IN – India, KH – Cambodia; LA – Laos; and VN – Vietnam. ([‡]) – Numbers (in parentheses) after Genbank accession numbers for *Cytb* and *COI* sequences of studied *Scotophilus* specimens are respective haplotypes representing in Figures 1 and 2. Reference ([§]): 1 – Francis et al., 2010; 2 – Ikram et al., unpublished; 3 – Kruskop et al., unpublished; 4 –Rahman & Choudhury, unpublished; 5 – Srinivasulu et al., unpublished; 6 – Tan et al., 2020; 7 – Trujillo et al., 2009; 8 – Tu et al., 2014; 9 – Tu et al., 2017; and 10 – Tu et al., 2018.

Taxon	Location ([†])	Genbank Accession No.				Ref ([§])
		<i>Cytb</i> ([‡])	<i>COI</i> ([‡])	<i>TUFM</i>	<i>ZFYVE27</i>	
<i>M. cyclotis</i>	Ngoc Linh, Kon Tum, VN	MH137367	KF772775	MH137554	MH137584	[8,10]
<i>E. pachyomus</i>	Copia, Son La, VN	KX496340	KX496341	KX496347	KX496346	[9]
<i>S. heathii</i>	Kohat, Khyber Pakhtunkhwa, Pakistan: 1	–	MG550115 (5)	–	–	[2]
<i>S. heathii</i>	Swabi, Khyber Pakhtunkhwa, Pakistan: 2	–	MH712738 (1)	–	–	[2]
<i>S. heathii</i>	Swabi, Khyber Pakhtunkhwa, Pakistan: 2	–	MH716035 (2)	–	–	[2]
<i>S. heathii</i>	Fateh Jang, Attock, Punjab, Pakistan: 3	–	MG199233 (4)	–	–	[2]
<i>S. heathii</i>	Fateh Jang, Attock, Punjab, Pakistan: 3	–	MG199234 (4)	–	–	[2]
<i>S. heathii</i>	Fateh Jang, Attock, Punjab, Pakistan: 3	–	MG199235 (4)	–	–	[2]
<i>S. heathii</i>	Fateh Jang, Attock, Punjab, Pakistan: 3	–	MG199236 (4)	–	–	[2]
<i>S. heathii</i>	Fateh Jang, Attock, Punjab, Pakistan: 3	–	MG199237 (4)	–	–	[2]
<i>S. heathii</i>	Fateh Jang, Attock, Punjab, Pakistan: 3	–	MG199238 (4)	–	–	[2]
<i>S. heathii</i>	Fateh Jang, Attock, Punjab, Pakistan: 3	–	MG199240 (4)	–	–	[2]
<i>S. heathii</i>	Fateh Jang, Attock, Punjab, Pakistan: 3	–	MG199241 (4)	–	–	[2]

Taxon	Location ^(†)	Genbank Accession No.				Ref ^(§)
		<i>Cytb</i> ^(‡)	<i>COI</i> ^(‡)	<i>TUFM</i>	<i>ZFYVE27</i>	
<i>S. heathii</i>	Fateh Jang, Attock, Punjab, Pakistan: 3	–	MG199242 (4)	–	–	[2]
<i>S. heathii</i>	Fateh Jang, Attock, Punjab, Pakistan: 3	–	MG544111 (4)	–	–	[2]
<i>S. heathii</i>	Fateh Jang, Attock, Punjab, Pakistan: 3	–	MG550114 (4)	–	–	[2]
<i>S. heathii</i>	Fateh Jang, Attock, Punjab, Pakistan: 3	–	MG199239 (4)	–	–	[2]
<i>S. heathii</i>	Fateh Jang, Attock, Punjab, Pakistan: 3	–	MF495678 (4)	–	–	[2]
<i>S. heathii</i>	Fateh Jang, Attock, Punjab, Pakistan: 3	–	MG299068 (4)	–	–	[2]
<i>S. heathii</i>	Hampi, Bellary, Karnataka, IN: 5	–	MG821185 (3)	–	–	[5]
<i>S. heathii</i>	-, Yunnan, China: 8	EU750946 (1)	–	–	–	[7]
<i>S. heathii</i>	Nam Et national protected area, LA: 9	–	HM541921 (7)	–	–	[1]
<i>S. heathii</i>	Nam Et national protected area, LA: 9	–	HM541922 (7)	–	–	[1]
<i>S. heathii</i>	Tam Dao, Vinh Phuc, VN: 12	EU750945 (2)	–	–	–	[7]
<i>S. heathii</i>	Ban Paam, Attapu, LA: 16	–	HM541920 (11)	–	–	[1]
<i>S. heathii</i>	Ban Paam, Attapu, LA: 16	–	HM541923 (17)	–	–	[1]
<i>S. heathii</i>	Dong Hua Sao, Champasak, LA: 17	–	HM541924 (14)	–	–	[1]
<i>S. heathii</i>	Dong Hua Sao, Champasak, LA: 17	–	HM541925 (14)	–	–	[1]
<i>S. heathii</i>	Yok Don NP, Dak Lak, VN: 20	–	HM541926 (15)	–	–	[1]
<i>S. heathii</i>	Yok Don NP, Dak Lak, VN: 20	EU750944 (3)	–	–	–	[7]
<i>S. kuhlii</i>	Tadlapet, Adilabad, Telangana, IN: 5	–	MG821195 (7)	–	–	[5]
<i>S. kuhlii</i>	Cachar, Assam, IN: 6	–	KT291764 (7)	–	–	[4]
<i>S. kuhlii</i>	Tam Dao, Vinh Phuc, VN: 12	EU750931 (16)	–	–	–	[7]

Taxon	Location ^(†)	Genbank Accession No.				Ref ^(§)
		<i>Cytb</i> ^(‡)	<i>COI</i> ^(‡)	<i>TUFM</i>	<i>ZFYVE27</i>	
<i>S. kuhlii</i>	Tam Dao, Vinh Phuc, VN: 12	EU750913 (13)	–	–	–	[7]
<i>S. kuhlii</i>	-, Guangxi, China: 13	LC426467 (18)	–	–	–	[6]
<i>S. kuhlii</i>	-, Guangxi, China: 14	LC426465 (17)	–	–	–	[6]
<i>S. kuhlii</i>	-, Guangxi, China: 14	LC426466 (17)	–	–	–	[6]
<i>S. kuhlii</i>	-, Guangxi, China: 14	LC426468 (17)	–	–	–	[6]
<i>S. kuhlii</i>	Savannakhet, LA: 15	–	HM541934 (16)	–	–	[1]
<i>S. kuhlii</i>	Cat Tien, Lam Dong, VN: 22	–	HM541935 (17)	–	–	[1]
<i>S. kuhlii</i>	Cat Tien, Lam Dong, VN: 22	–	HM541936 (19)	–	–	[1]
<i>S. kuhlii</i>	Cat Tien, Lam Dong, VN: 22	EU750924 (24)	–	–	–	[7]
<i>S. kuhlii</i>	Cat Tien, Lam Dong, VN: 22	–	HM541937 (13)	–	–	[1]
<i>S. kuhlii</i>	Cat Tien, Lam Dong, VN: 22	EU750925 (10)	–	–	–	[7]
<i>S. kuhlii</i>	Cat Tien, Lam Dong, VN: 22	–	HM541938 (11)	–	–	[1]
<i>S. kuhlii</i>	Cat Tien, Lam Dong, VN: 22	EU750926 (20)	–	–	–	[7]
<i>S. kuhlii</i>	Cat Tien, Lam Dong, VN: 22	–	HM541940 (9)	–	–	[1]
<i>S. kuhlii</i>	Cat Tien, Lam Dong, VN: 22	–	JF444113 (10)	–	–	[3]
<i>S. kuhlii</i>	Cat Tien, Lam Dong, VN: 22	–	JF444114 (8)	–	–	[3]
<i>S. kuhlii</i>	Cat Tien, Lam Dong, VN: 22	EU750923 (19)	–	–	–	[7]
<i>S. kuhlii</i>	Cat Tien, Lam Dong, VN: 22	EU750927 (21)	–	–	–	[7]
<i>S. kuhlii</i>	Ho Chi Minh, VN: 23	–	HM541927 (20)	–	–	[1]
<i>S. kuhlii</i>	Soc Trang, Soc Trang, VN: 24	–	HM541929 (21)	–	–	[1]

Taxon	Location ^(†)	Genbank Accession No.				Ref ^(§)
		<i>Cytb</i> ^(‡)	<i>COI</i> ^(‡)	<i>TUFM</i>	<i>ZFYVE27</i>	
<i>S. kuhlii</i>	Soc Trang, Soc Trang, VN: 24	–	HM541932 (22)	–	–	[1]
<i>S. kuhlii</i>	Soc Trang, Soc Trang, VN: 24	EU750930 (27)	–	–	–	[7]
<i>S. kuhlii</i>	Soc Trang, Soc Trang, VN: 24	–	HM541933 (21)	–	–	[1]
<i>S. kuhlii</i>	Soc Trang, Soc Trang, VN: 24	EU750929 (23)	–	–	–	[7]
<i>S. kuhlii</i>	Soc Trang, Soc Trang, VN: 24	–	HM541930 (18)	–	–	[1]
<i>S. kuhlii</i>	Soc Trang, Soc Trang, VN: 24	–	HM541931 (1)	–	–	[1]
<i>S. kuhlii</i>	Jitra, Kedah State, Malaysia: 27	EU750920 (19)	–	–	–	[7]
<i>S. kuhlii</i>	Jitra, Kedah State, Malaysia: 27	EU750922 (25)	–	–	–	[7]
<i>S. kuhlii</i>	Jitra, Kedah State, Malaysia: 27	EU750915 (26)	–	–	–	[7]
<i>S. kuhlii</i>	- , Luzon Island, Philippines: 28	EU750914 (17)	–	–	–	[7]

Table S3. Primers used to amplify and sequence DNA in the present study

Gene	Primer sets (5'-3')	Amplicon length (bp)	Sources
<i>Cytb</i>	Mt-L14724F: CGAGATCTGAAAAACCATCGTTG Cytb-H15915R: AACTGCAGTCATCTCCGGTTTACAAGA	~ 1190	Irwin, Kocher, & Wilson, 1991.
	Cy-14726F: GACYARTRRCATGAAAAAYCAYCGT TGT Cy- 15909R: CYCWTYIYTGGTTTACAAGACYAG	~ 1180	Arai et al., 2016
<i>COI</i>	MammMt-5533F: CYCTGTSYTTTTRATTTACAGTYAA MammMt-7159R: GRGGTTCRAWWCCTYCCTYTCTT	~ 1620	Arai et al., 2019
	UTyr: ACCYCTGTCYTTAGATTTACAGTC C1L705: ACTTCDGGGTGNCCRAARAATCA	~ 750	Hassanin et al., 2013
<i>TUFM</i>	TUFM-EX9U: CTGACTTGGGACATGGCCTGTCTG TUFM-EX10L: ACGCTGGCCTTTYTCTAAGATCAT	~ 700	Hassanin et al., 2013
<i>ZFYVE27</i>	ZFYVE27-EX6U: GAATGTGGAGTTCTTCCGAG ZFYVE27-EX7L: GGGTTCATCCGCCGCTGCAGA	~ 750-800	Hassanin et al., 2013

Table S4. mtDNA divergence within Asian *Scotophilus* spp.

	<i>S. kuhlii</i> s.l.		<i>S. heathii</i> s.l	
	<i>COI</i> (576nt)	<i>Cytb</i> (1140nt)	<i>COI</i> (576nt)	<i>Cytb</i> (1140nt)
Number of locations	13	10	13	6
Number of sequences	43	46	39	12
Number of segregating sites	41	69	69	78
Number of haplotypes	22	27	18	7
Haplotype diversity (Hd)	0.932	0.922	0.865	0.879
Nucleotide diversity (π)	0.013	0.010	0.034	0.025

Table S5. *COI* genetic variation in three clusters of geographic populations of *S. heathii* s.l..**S5A - mtDNA divergence within three populations of *S. heathii*.**

	Indian Subcontinent (Pakistan + India)	Northern Indochina	Southern Indochina
Number of locations	4	4	6
Number of sequences	18	8	13
Number of segregating sites	16	5	20
Number of haplotypes	5	4	9
Haplotype diversity (Hd)	0.405	0.821	0.95
Nucleotide diversity (π)	0.0038	0.0035	0.01

S5B - Molecular variance (AMOVA) of *COI* variation in three populations of *S. heathii* s.l..

Source of variation	d.f.	SSD	Variance component	% variation	F-statistics	P values
Within populations	36	24.024	0.334	68.7	Fis=1.000	0.001
Among populations	2	8.848	0.152	31.3	Fst=0.313	0.001

S5C - Pairwise estimates of F_{ST} (below diagonal) and closest geographic distances (Km) (above diagonal) between three geographic populations of *S. heathii* s.l..

	Indian Subcontinent (Pakistan + India)	Northern Indochina	Southern Indochina
Indian Subcontinent (Pakistan + India)		2903	3116
Northern Indochina	0.433***		589
Southern Indochina	0.343***	0.11**	

*** – $p \leq 0.001$; ** – $0.001 \leq p \leq 0.05$

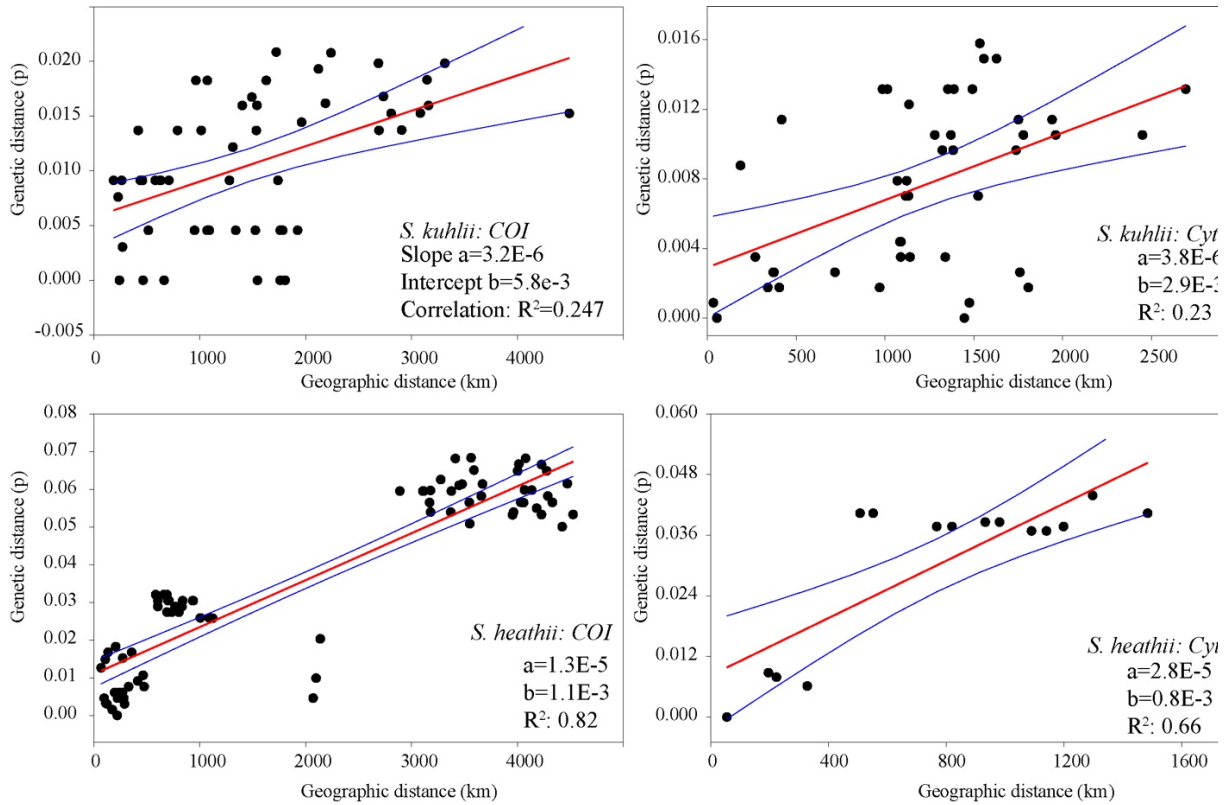
Table S6. Factor loading for two first PCs from PCA of cranial characters.

Characters	PC 1	PC 2
GSL	0.3500	-0.2112
SL	0.3374	-0.3527
CBL	0.2997	-0.1891
CCL	0.3054	-0.0987
ZB	0.3346	-0.2892
C¹C¹	0.3356	0.7576
M³M³	0.2881	0.0963
CM³	0.2835	0.2506
ML	0.3161	-0.1212
CM₃	0.3045	0.2030
Eigenvalue	0.0106	0.0003
% variance	94.184	2.3724

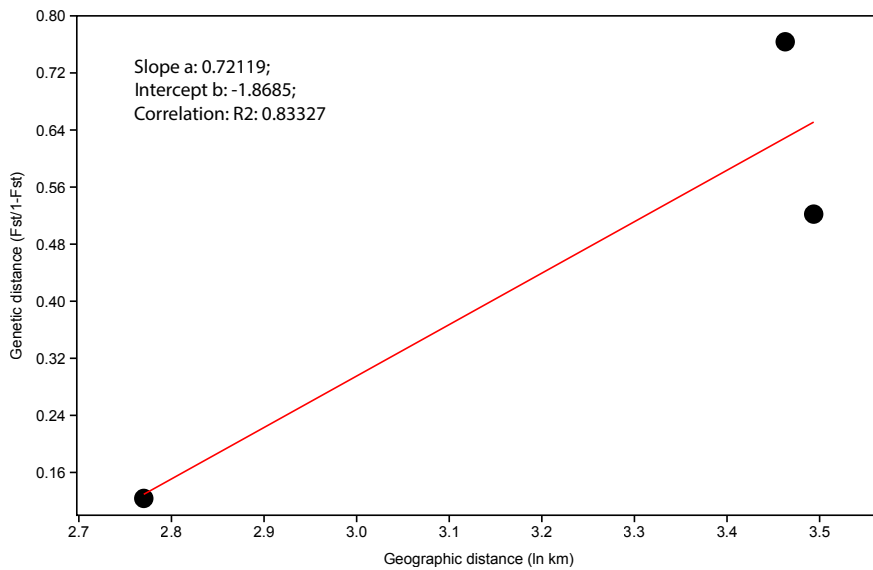
Table S7. Pairwise comparisons (ANOVA-tests) of morphometrics among geographical populations of *S. heathii* s.l. in Indochina.
Acronyms and definitions for measurements are given in the Materials and Methods.

Character	North VN			Highland Central VN		South Central VN
	Highland Central VN (Location: 18)	South Central (Location: 21 and nearby)	Cambodia (Location: 19)	South Central (Location: 21 and nearby)	Cambodia (Location: 19)	Cambodia (Location: 19)
FA		***		***	***	_*
Tib				***	***	
GSL	_***	**		***	***	
SL	_***	**		***	***	
CBL	_***	***		***	***	_*
CCL	_***	***		***	***	_*
ZB	_***	**		***	***	_**
C ¹ C ¹		***		**		
M ³ M ³		**		***	**	
CM ³		***	**	***	***	_*
ML	_**	***		***	***	_*
CM ₃		***		***	**	_*

Level of statistical significance: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.



A: Correlation between pairwise genetic divergences (minimum p-distance) and geographic distance (km) among geographic populations of Asian *Scotophilus* spp.



B: Correlation between pairwise genetic divergences and geographic distance among three groups of matriline of *S. heathii* inferred from the COI TCS network analyses

Figure S1: Mantel tests for isolation by distance effects on pairwise genetic divergences among geographic populations of studied *Scotophilus* spp.

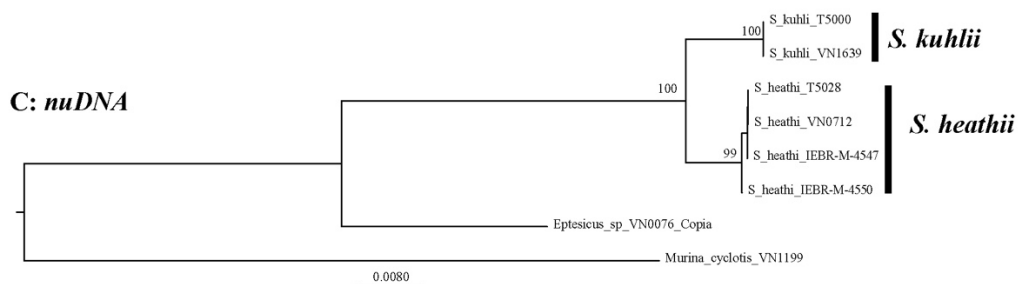
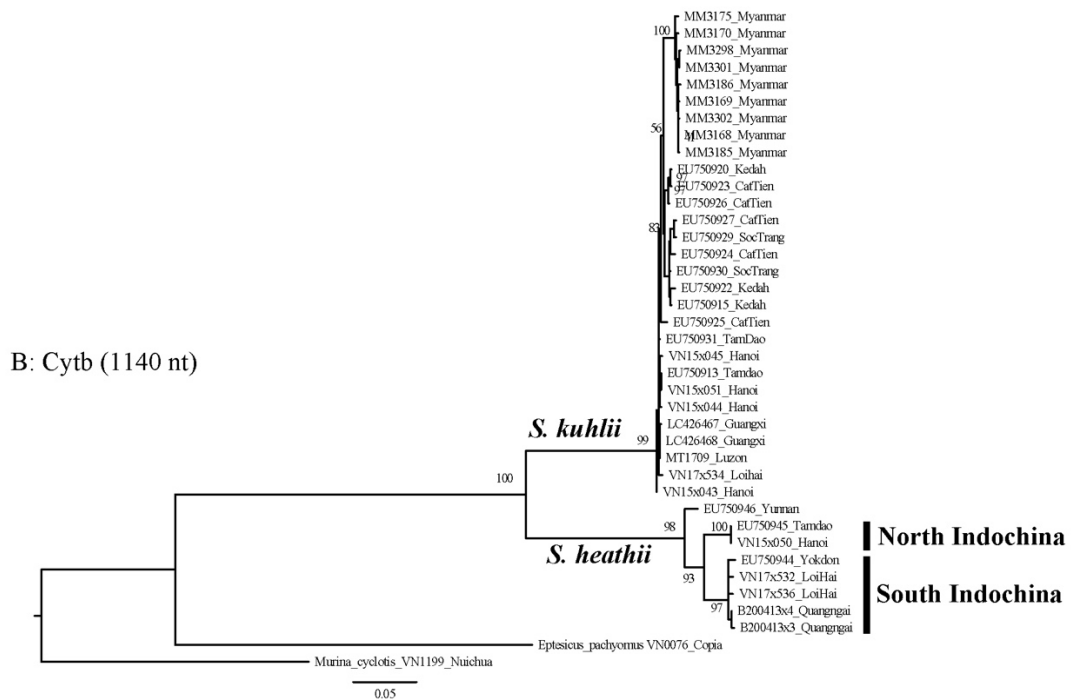
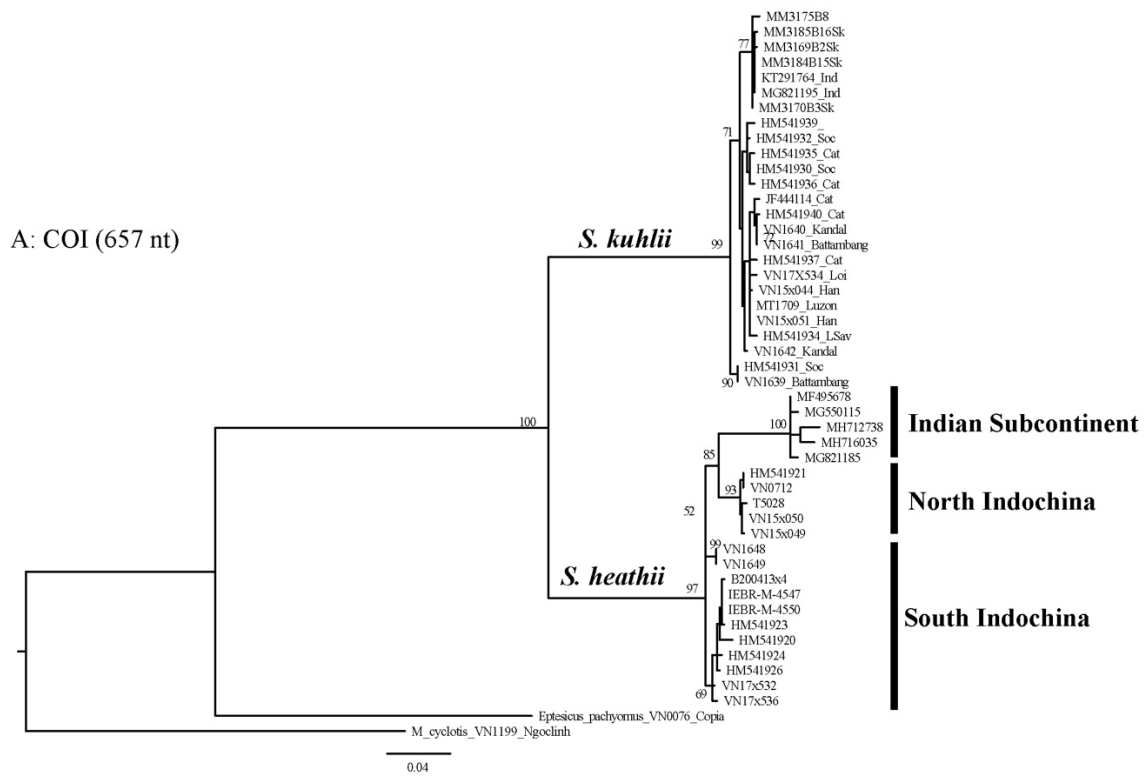
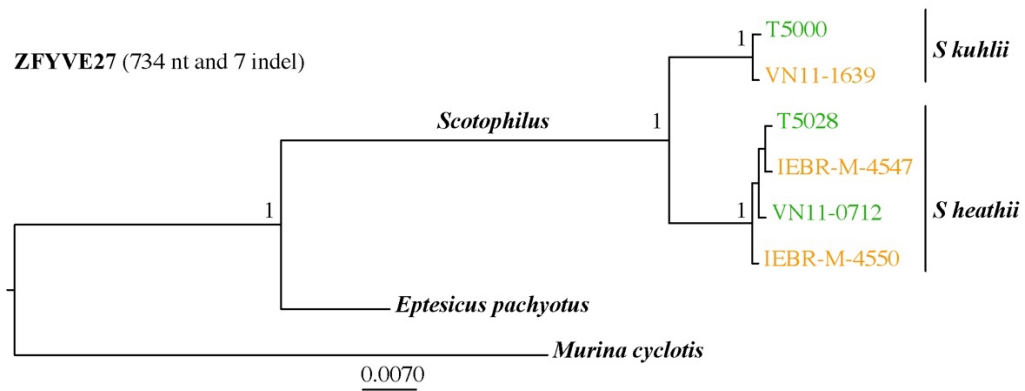
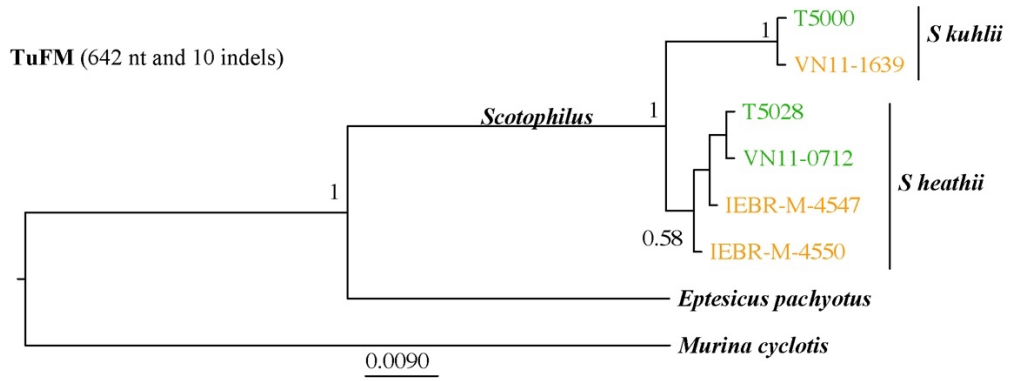


Figure S2. ML trees of Asian *Scotophilus* spp. and outgroups reconstructed from *COI*, *Cytb* and *nuDNA* sequences.

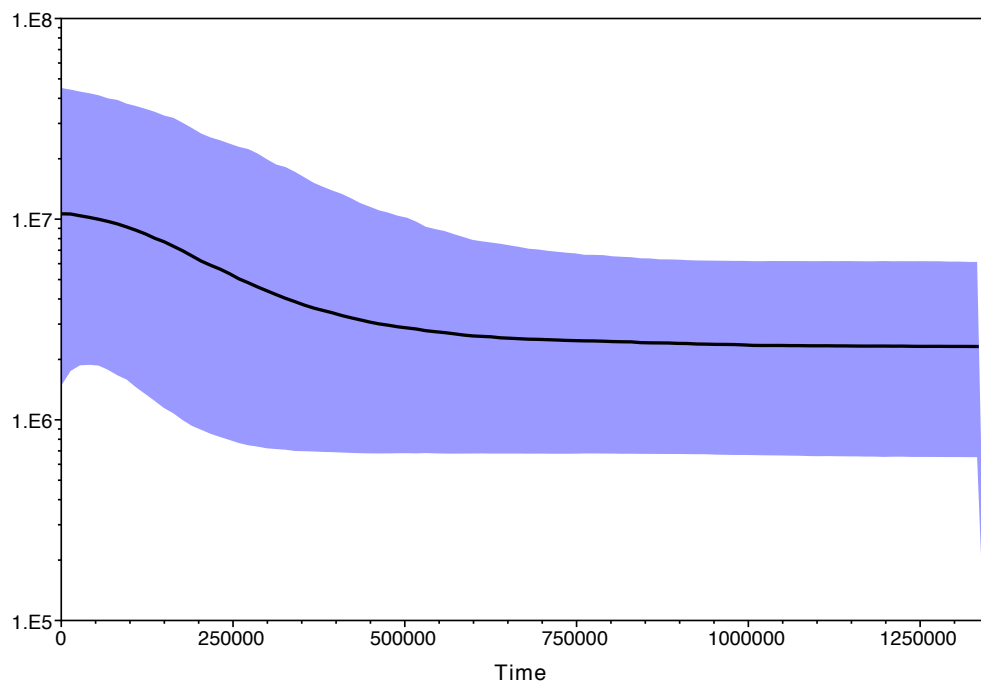
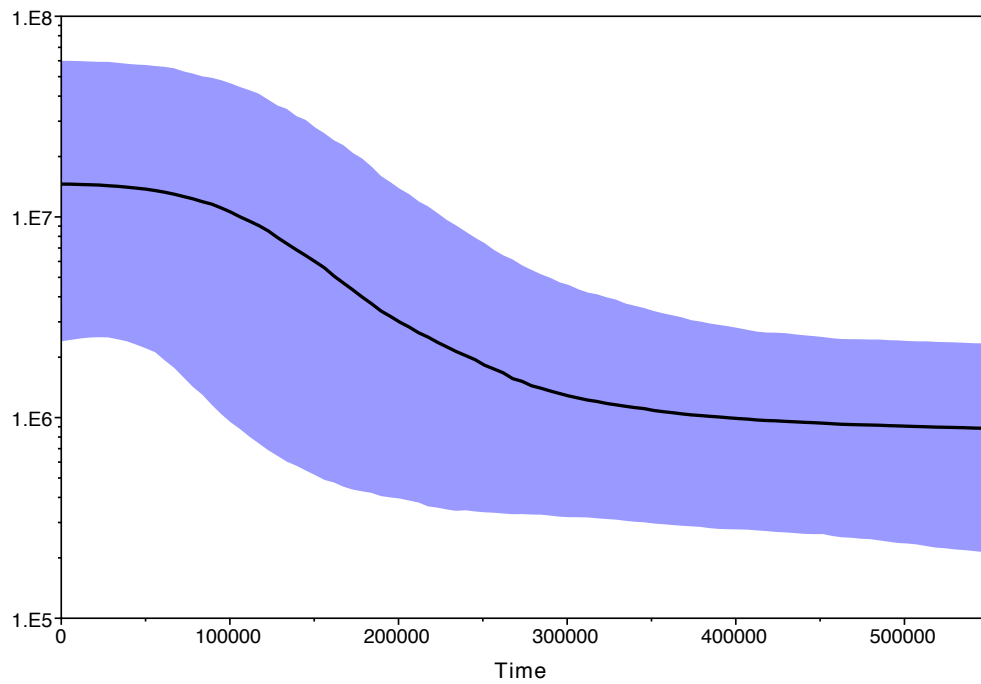
0
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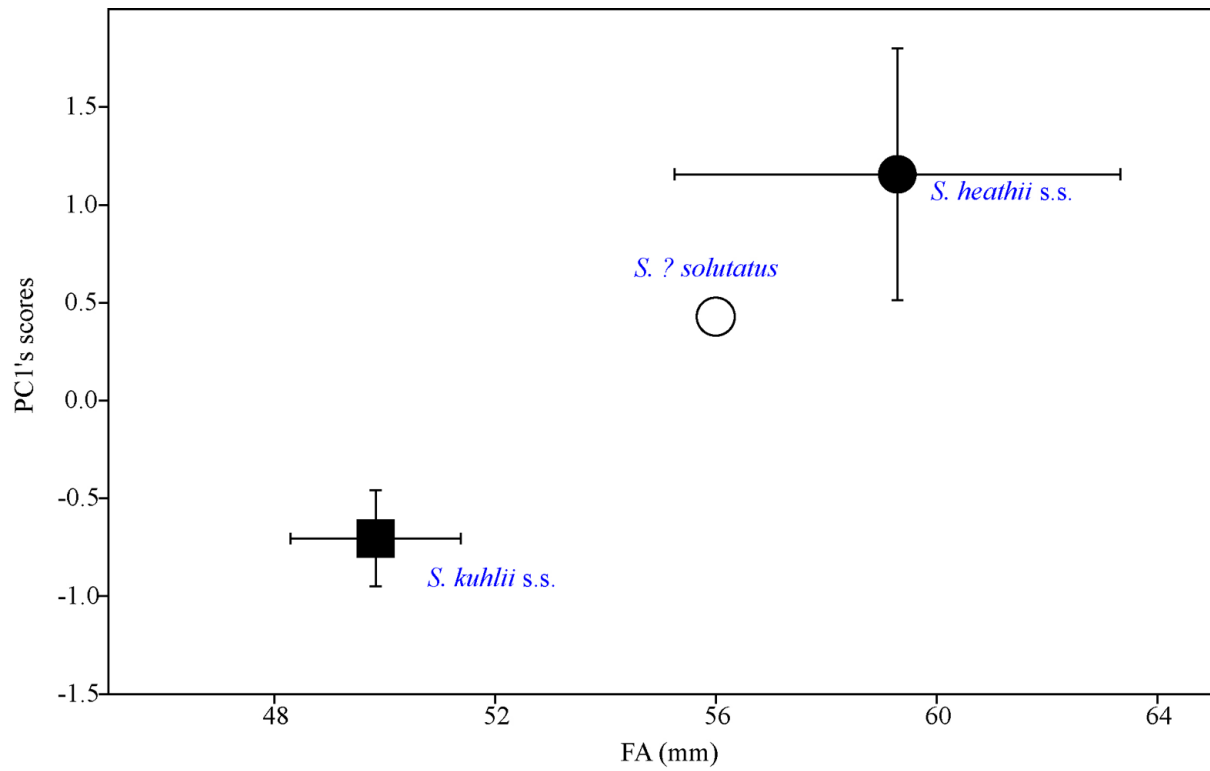


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Figure S3. Bayesian trees of Asian *Scotophilus* spp. and outgroups reconstructed from *TUFM* and *ZFYVE27* sequences



9 **Figure S4. Bayesian skyline plot representing historical demographic trends in *S. kuhlii***
 10 **(above) and *S. heathii* (below).** The *X*-axis presents time as years before present. The *Y*-axis
 11 represents the effective female population size (N_e). Mean estimated N_e represents as the
 12 solid line, whereas solid intervals refer the 95% highest probability density.



13

14 **Figure S5. Correlation between mean values of PC1's scores obtained from PCA of skull**
 15 **characters and FA values of Asian *Scotophilus* spp.**

16

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