


Integrative taxonomy of the *Rhinolophus macrotis* complex (Chiroptera, Rhinolophidae) in Vietnam and nearby regions

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Abstract

The taxonomic status of *Rhinolophus macrotis* sensu lato (s.l.) in Vietnam and adjacent territories remains problematic. To address this issue, we performed an integrated study of morphological, acoustic, and genetic characters of *R. macrotis* s.l. specimens and compared these with sympatric species within the *philippinensis* group (*R. marshalli*, *R. paradoxolophus*, and *R. rex*). Our results reveal that in addition to a cryptic species of *R. macrotis* previously found in Jiangxi and Jingmen, China, *R. macrotis* s.l. in continental Asia includes three further species, namely *R. cf. siamensis*, *R. cf. macrotis*, and *R. cf. macrotis* "Phia Oac." These four taxa are distinguished from genuine *R. macrotis* in Nepal and *R. siamensis* in Thailand by their morphological and/or genetic features. Further taxonomic evaluation of the subspecies of *R. macrotis* s.l. is needed to determine their affinities with recently recognized cryptic species and to possibly describe new taxa. Our results also show that interspecific divergences in mitochondrial DNA sequences (*Cytb* and *COI* genes) among taxa within the *philippinensis* group (particularly between *R. cf. siamensis*/*R. cf. macrotis* and *R. rex*/*R. paradoxolophus*) are significantly lower than those of other morphological groups in the genus. These phylogenetic patterns might be explained by recent allopatric speciation or ancient introgression events among ancestors of the taxa during the Pleistocene. However, further investigations including genetic analyses of nuclear genes are needed to test the latter hypothesis.

KEYWORDS

Acoustics, biogeography, Morphology, mtDNA, phylogeny, *Rhinolophus*, Taxonomy

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1 | INTRODUCTION

The big-eared horseshoe bat, *Rhinolophus macrotis* Blyth, 1844; was originally described from the Kathmandu Valley in Nepal as a small species within Rhinolophidae (Blyth, 1844). The taxon is differentiated from other horseshoe bats by external features (i.e., very large ears, long, broad, and tongue-shaped sella, and a well-developed lancet with a rounded tip) and skull characteristics (i.e., long palatal bridge, weak upper canines, and well-developed anterior nasal swellings) (Csorba, Ujhelyi, & Thomas, 2003).

Rhinolophus macrotis s.l. shares several primitive characters (e.g., the wing structure with subequal metacarpals, long palatal bridge, and middle lower premolar [P₃] often situated in the toothrow) with sister species within the *philippinensis* group including the following: *R. philippinensis* Waterhouse, 1843; *R. marshalli* Thonglongya, 1973; *R. rex* Allen, 1923; and *R. paradoxolophus* Bourret, 1951 (Andersen, 1905, 1907; Bogdanowicz, 1992; Bogdanowicz & Owen, 1992; Csorba et al., 2003; Tate, 1943). Since its original description, three additional subspecies of *R. macrotis* have been described from different localities in Asia: *R. m. dohrni* Andersen, 1907 (type locality [t.l.]: Soekaranda, Deli, Sumatra), *R. m. siamensis* Gyldenstolpe, 1917 (t.l.: Doi Par Sakang, northwestern Thailand), and *R. m. topali* Csorba & Bates, 1995 (t.l.: Kakul phosphate mine, Abbottabad, Pakistan). Tate (1943) subsumed further three taxa which were originally described as distinct species or subspecies under *R. macrotis*: *R. hirsutus* Andersen, 1905 (t.l.: Guimaras Island, Philippines), *R. episcopus* Allen, 1923 (t.l.: Wanshien, Sichuan, China), and *R. e. caldwelli* Allen, 1923 (t.l.: Yuki, Fukien, China). Based on this classification, *R. macrotis* has been considered widespread in Asia (Figure 1) (Corbet & Hill, 1992; Csorba et al., 2003; Molur, Srinivasulu, & Francis, 2008).

Ingle and Heaney (1992) suggested that *R. m. hirsutus* in the Philippines should be re-elevated to species rank due to its morphological differences from other subspecies of *R. macrotis*. Because this view is supported by Guillén-Servent, Francis, and Ricklefs (2003), who showed that *R. m. hirsutus* is more closely related to the Philippine *R. philippinensis* lineage and distinct from Indochinese *R. macrotis*, the presence of *R. macrotis* s.l. in the Philippines should be discounted. In Indochina, Osgood (1932) found two morphologically distinct subspecies of *R. macrotis* s.l. in sympatry and parapatry in northwest Vietnam: The larger bat with a forearm length (FA) of 43.3–45.3 mm was identified as *R. macrotis caldwelli* (originally *R. episcopus caldwelli*), whereas the smaller bat (FA: 38–39 mm) has hitherto been allocated to *R. m. siamensis* (although it is intermediate

between genuine *R. m. macrotis* [FA: 41–43 mm] and *R. m. siamensis* [FA: 36.1 mm] from their respective type localities in Nepal and Thailand). In Laos, Francis, Guillén-Servent, and Robinson (1999) found that sympatric specimens of *R. m. siamensis* and *R. m. caldwelli* are very similar genetically, but can be differentiated by body and skull size, noseleaf structure, and echolocation calls. As a consequence, Francis (2008) and subsequent authors (Kruskop, 2013; Thomas, Duckworth, Douangboubpha, Williams, & Francis, 2013) subsumed bats with a FA of 42–47 mm and lower echolocation calls with frequencies of maximum energy (FmaxE) of ca. 51–52 kHz (in Laos) into *R. macrotis*, whereas *R. siamensis* has been regarded as a smaller form with a FA of 38–42 mm that emits higher echolocation calls (FmaxE: 67–74 kHz in Laos).

Rhinolophus siamensis and *R. macrotis* occur in sympatry in many localities in China (Figure 1). The former taxon is smaller with a FA of 36–41 mm, whereas the latter is usually larger with a FA of 39–48 mm (Smith et al., 2008). However, Sun et al. (2008) concluded that bats of *R. macrotis* s.l. at different localities in southern China can be divided into three different phenetic and phonic forms: (i) a large form in Jiangxi Province (C6 in Figure 1) characterized by an average FA of >45 mm and a mean FmaxE of 48.8 kHz; (ii) a small form in Jiangxi (C6 in Figure 1) and Guangxi provinces (C5 in Figure 1) with a mean FA of <40 mm and mean FmaxE of 64.7–66.7 kHz; and (iii) an intermediate form in Yunnan Province (C1 in Figure 1) with a mean FA of 42.3–43.5 mm and a mean FmaxE of 57.3 kHz. Genetic divergence of cytochrome b (*Cytb*) sequences between the large form and two other forms was comparable with that between *R. macrotis* s.l. and *R. rex*, whereas divergence between the two latter forms was <2%. Sun et al. (2008) consequently suggested that the large form may represent a cryptic species of *R. macrotis*, whereas the slight differences in morphology and echolocation calls between the two other forms were attributed to geographic variation rather than speciation. Wu, Motokawa, and Harada (2008) considered records of *R. siamensis* in China erroneous and hence described southern Chinese specimens formerly identified as *R. siamensis* as a new species, *R. huananus* Wu et al., 2008;. Zhang et al. (2009) subsequently regarded *R. huananus* as a junior synonym of *R. siamensis* and provided criteria to discriminate the latter taxon from *R. macrotis* in China as follows: “Bats with FA >46 mm and FmaxE <55 kHz were assigned to *R. macrotis*. If FA <46 mm and FmaxE >58 kHz, then bats were assigned to *R. siamensis*.”

Since 2002, *R. macrotis* s.l. specimens collected in different localities of Vietnam have been identified as *R. cf. macrotis* or *R. cf.*

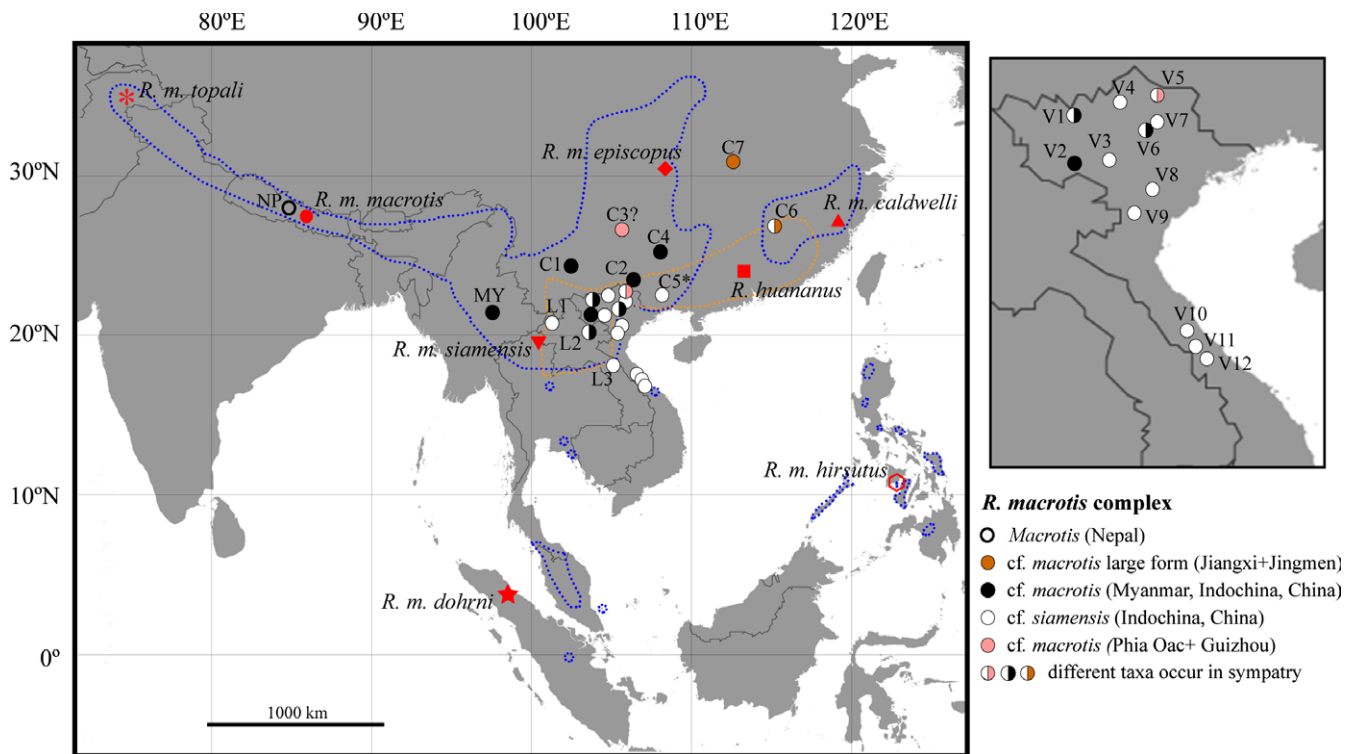


FIGURE 1 Distribution areas of *Rhinolophus macrotis* s.l. (blue dot line) and *R. siamensis* (orange dot line) in Asia (Chiozza, 2008; Molur et al., 2008) and taxonomic sampling used for this study. Red symbols are type localities of described taxa of the *R. macrotis* complex. The localities of bats of the *R. macrotis* complex collected by previous studies are presented in large map, and those collected by the authors in Vietnam are detailed in small map: NP—Pokhara, Nepal; MY—Myanmar; C—China: C1—Jinning County, Yunnan (originally *R. macrotis* s.l. intermediate form (Sun et al., 2008)); C2—Vicinity Of Nian Wei, Guangxi; C3—imprecise locality, Guizhou; C4—Shuipu Village, Libo, Guizhou; C5—Nanning city, Guangxi; C6—Jinggangshan Nature Reserve (NR), Jiangxi; C7—, Jingmen; L—Laos: L1—Ban En, Luang Namtha; L2—NamEt NBCA, Louangphrabang; L3—Lak Sao, Khammouan; V—Vietnam: V1—Hoang Lien National Park (NP), Lao Cai; V2—Copia NR, Son La; V3—Xuan Son NP, Phu Tho; V4—Khou Ca NR, Ha Giang; V5—Phia Oac—Phia Den NR, Cao Bang; V6—Na Hang NR, Tuyen Quang; V7—Ba Be NP, Bac Kan; V8—Cuc Phuong NP, Ninh Binh; V9—Xuan Lien NR, Thanh Hoa; V10—Phong Nha-Ke Bang NP, Quang Binh; V11—Bac Huong Hoa NR, Quang Tri; and V12—Dakrong NR, Quang Tri

siamensis based on their body size and/or echolocation calls following Francis (2008). However, in 2015 and 2016, three specimens of *R. cf. macrotis* were collected in Phia Oac–Phia Den Nature Reserve, Cao Bang Province (hereafter Phia Oac) (Figure 1), which could be differentiated from other forms by their significantly larger body size, other external characters (e.g., ears and noseleaf structure) (Tu et al., 2016), and echolocation call parameters. Because considerable discrepancies remain in criteria for identifying *R. macrotis* and *R. siamensis* in Indochina and southern China, we examine the taxonomic status of Vietnamese taxa within the *R. macrotis* complex based on analyses of their morphological characteristics, acoustic parameters, and mitochondrial DNA sequences.

2 | MATERIALS AND METHODS

2.1 | Morphological analyses

We examined 60 specimens of *R. macrotis* s.l. ($n = 42$), *R. marshalli* ($n = 5$), and *R. paradoxolophus* ($n = 13$) collected during field surveys in Vietnam between 2002 and 2016 (Figure 1; Appendix 1). All

specimens are held in the Institute of Ecology and Biological Resource, Vietnam Academy of Science and Technology, Hanoi, Vietnam (IEBR). All specimens examined were adults, as confirmed by the presence of fully ossified metacarpal–phalangeal joints.

External measurements were taken to the nearest 0.1 mm from alcohol-preserved specimens. These included the following: FA—length of forearm; Tail—tail length; E—ear length; Tib—tibia length, from the knee joint to the ankle; HF—hind foot length, from the tarsal joint to the outermost part of the claw of the longest finger; HSW—greatest width of anterior noseleaf; SHE—height of sella, from the cup at the base; SEW—width of sella at the middle; 3rd^{mt}—length of the third metacarpal; 4th^{mt}—length of the fourth metacarpal; and 5th^{mt}—length of the fifth metacarpal.

Craniodental measurements were taken to the nearest 0.01 mm using digital callipers under a stereomicroscope. These included the following: GLS—total length of skull, from the most anterior part of the premaxillae to the occiput; SL—greatest length of skull, from the most anterior part of the upper canine to the most posteriorly projecting point of the occipital region; CCL—condylo-canine length, from the exoccipital condyle to the most anterior part of the canine;

ZB—greatest width of the skull across the zygomatic arches; MB—greatest distance across the mastoid region; ALSW—greatest width of the anterior lateral swellings in dorsal view; AMSW—width of the anterior median swellings in the dorsal view; C¹C¹—greatest width across the upper canines between their buccal borders; M³M³—greatest width across the crowns of the last upper molars; PL—length of palatal bridge; IC—width of interorbital constriction; CM³—maxillary toothrow length, from the anterior of the upper canine to the posterior of the crown of the 3rd upper molar; ML—length of mandible, from the anterior rim of the alveolus of the first lower incisor to the most posterior part of the condyle; and CM₃—mandibular toothrow length, from the anterior of the lower canine to the posterior of the crown of the 3rd lower molar.

To test the phenetic affinities of the studied specimens, principal component analysis (PCA) was performed in PAST (Hammer, Harper, & Ryan, 2001) on the log-transformed morphometric measurements (data of different sexes were combined). Using the original descriptions of recognized subspecies or synonyms of *R. macrotis* s.l. in mainland Asia (*R. siamensis*, *R. episcopus*, *R. e. caldwelli*, *R. m. topali*, and *R. huananus*: Gyldenstolpe, 1917; Allen, 1923; Csorba & Bates, 1995; Wu et al., 2008), we evaluated the phenetic affinities of our material and these taxa using PCA on seven craniodental measurements: SL, ZB, MB, CM³, M³M³, ML, and CM₃. As these measurements are standard in bat research and vary little between observers, comparisons using these data from different sources can be performed with reasonable confidence (Palmeirim, 1998). Prior to the analysis, data were scaled to the same precision of measurements from the literature. The equalities of mean values of all morphological measurements and PC scores obtained from PCA between different taxa were tested using a one-way analysis of variance (ANOVA), followed by a Tukey HSD multiple comparison test for unequal sample sizes (Tukey–Kramer) or a Kruskal–Wallis test (Zar, 1999).

To examine the glans penis, digital 2D images were taken using a Leica M80 binocular microscope connected to a PC. To examine bacula, 5% potassium hydroxide was used to macerate the skin and ossified tissues, which were then removed manually. A small quantity of alizarin red was added during maceration to stain examined materials. Following dissection, bacula were stored in glycerin (Frisley, 1947). Digital 2D images of bacula were taken using the same apparatus and from which the following measurements (as detailed in Figure 6) were taken to the nearest 0.01 mm using Leica Acquire Software version 3.3 (Leica Microsystems Ltd, Switzerland): total length; height of basal cone; width of basal cone; and width of tip.

2.2 | Acoustic analyses

Between 2006 and 2014, echolocation calls of bats held in the hand or resting in a flight tent were recorded with a Pettersson D240x bat detector with a sampling frequency of 307 kHz (Pettersson Elektronik, Sweden) and stored digitally on an Edirol R-09HR recorder (Roland, USA). In 2016, bat calls were recorded by an Echo Meter

Touch (Wildlife Acoustics, USA), connected to an iPhone 5S (Apple, USA).

The properties of all recorded calls were analyzed by callViewer v.18 (Skowronski, 2008). For each bat, we calculated the mean value \pm SD of the frequency of maximum energy (FmaxE), the start and end frequency (SF and EF), the sound duration (ms), and inter-pulse interval (IPI) from 5 to 10 calls. We also tabulated the same metrics reported for species within the “*R. philippinensis*” group (*R. macrotis*, *R. marshalli*, *R. paradoxolophus*, and *R. rex*) elsewhere in mainland Asia to determine inter- and intraspecific variation in their echolocation calls.

2.3 | Genetic analyses

Eighteen tissue samples of morphologically identified specimens of *R. macrotis* s.l. ($n = 15$), *R. marshalli* ($n = 1$), and *R. paradoxolophus* ($n = 2$) were collected in Vietnam between 2011 and 2016. Tissue samples were taken from the chest muscles of voucher specimens or from the patagium (biopsy punches; 3 mm diameter) of released bats and preserved in 95% ethanol. Samples were stored at -20°C until processing. Total DNA was extracted using QIAGEN DNeasy Tissue Kit (Qiagen, Germany) in accordance with the manufacturer's instructions. Two mitochondrial genes were sequenced in three laboratories (the Centre National de Séquençage, France; the Biological Research Centre of the Hungarian Academy of Sciences, Hungary; and the Infectious Disease Surveillance Center, Japan) for this study: the complete cytochrome b (*Cytb*; 1,140 bp) and the 5' fragment of cytochrome c oxidase subunit I (*COI*; 657 bp). Primer sets used for PCR amplification of *Cytb* were Mt-14724F/Cyb-15915R (Irwin, Kocher, & Wilson, 1991), Cy-14726F/Cyb-15909R (Arai et al., 2016), or Molcit-F/Cytc-H (Ibáñez, García-Mudarra, Ruedi, Stadelmann, & Juste, 2006; Weyeneth, Goodman, Stanley, & Ruedi, 2008) and of *COI* were UTyr/C1L705 (Hassanin et al., 2012) or VF1d/VR1d (Ivanova, Zemplak, Hanner, & Hebert, 2007) (Table S3).

PCR amplifications of *Cytb* and *COI* genes were performed as detailed in Tu et al. (2015), Arai et al. (2012), and Lim et al. (2016). PCR products were purified using ExoSAP Kit (GE Healthcare, UK) and sequenced in both directions with the PCR primers. The sequences obtained were then edited and assembled using CodonCode Alignment version 3.7.1 (CodonCode Corporation, USA) and Genetyx v11 software (Genetyx Corporation, Japan). The sequences were deposited in GenBank under the accession numbers KY652895–KY652914 (Appendix 1).

To explore the phylogenetic relationships of our material and allied species in continental Asia, our analyses included additional *Cytb* and *COI* sequences of *R. macrotis*, *R. marshalli*, *R. paradoxolophus*, and *R. rex* available in the GenBank database. The origins of all samples are presented in the Table S4, but only those of *R. macrotis* s.l. are denoted in Figure 1. As a consequence, phylogenetic trees of *R. macrotis* s.l. in continental Asia were inferred from two separate mitochondrial datasets: (i) *Cytb* (37 sequences and 1140 nt) and (ii) *COI* (36 sequences and 657 nt), both using Bayesian inference (BI) with MrBayes v3.2 (Ronquist et al., 2012). Following Guillén-Servent

et al. (2003), out-groups included *Coelops frithii* Blyth, 1848, and *Aseliscus dongbacana* Tu et al., 2015 of the Hipposideridae, and two species of the genus *Rhinolophus*, *R. pearsonii* Horsfield, 1851, and *R. pusillus* Temminck, 1834 (Table S4). Sequences were aligned manually in PhyDe version 0.9971 (Müller, Müller, Neinhuis, & Quandt, 2010). No gaps and stop codons were found in the alignments of the mitochondrial *COI* and *Cytb* protein-coding genes. The best-fitting models of sequence evolution for *Cytb* (GTR+I+G) and *COI* (GTR+I) datasets were selected with jModelTest v2.1.4, using the Akaike information criterion (Darriba, Taboada, Doallo, & Posada, 2012). Posterior probabilities (PPs) were calculated using four independent Markov chains run for 10,000,000 Metropolis-coupled MCMC generations, with trees sampled every 1,000 generations, and a burn-in rate of 25%. Uncorrected pairwise genetic distances (p-distances) were calculated with PAUP* version 4b10 (Swofford, 2003).

3 | RESULTS

3.1 | Morphology

Among Vietnamese members of the *philippinensis* group, *R. paradoxolophus* and *R. marshalli* could be unequivocally differentiated from *R. macrotis* s.l. by external and craniodental characters (Figures 2 and 3, Table 1). *Rhinolophus macrotis* s.l. specimens collected in Phia Oac (hereafter *R. cf. macrotis* Phia Oac) were distinguishable from specimens collected in other localities by their larger body and skull sizes, and noseleaf structure. Remaining *R. macrotis* s.l. specimens were subdivided into two separate forms, namely *R. cf. macrotis* and *R. cf. siamensis* (Figures 2 and 3, Table 1). The phenetic affinities of specimens were confirmed among these five taxa by PCAs on external and craniodental measurements (Data S1).

A PCA on seven craniodental measurements of our material and recognized subspecies or synonyms of *R. macrotis* s.l. in mainland Asia (including *R. siamensis*, *R. episcopus*, *R. e. caldwelli*, *R. m. topali*, and *R. huananus*: Gyldenstolpe, 1917; Allen, 1923; Csorba & Bates, 1995; Wu et al., 2008) revealed two PCs showing significant differences between taxa (ANOVA: $P < 0.05$) (Figure 4). PC1 (accounted for 97.6% of total variance) correlated positively with all seven characters and reflects size in general, whereas PC2 (accounted for 1.0% of total variance) with high factor loading for M^3M^3 , MB, and ZB reflects shape (see Table 2). In the plot of PC1 against PC2 (Figure 4), *R. paradoxolophus* and *R. marshalli* were separated from *R. macrotis* s.l. Within the latter taxon, PC1 shows that *R. siamensis* is the smallest taxon, whereas *R. cf. macrotis* Phia Oac is the largest and *R. cf. siamensis* and *R. huananus* appear in an overlapping cluster, intermediate between *R. siamensis* and *R. e. caldwelli*. *Rhinolophus cf. macrotis* is intermediate between *R. e. caldwelli* and *R. m. topali*, whereas *R. episcopus* is slightly larger than *R. m. topali*, but distinctly smaller than *R. cf. macrotis* Phia Oac. Based on PC2, two separate groups can be observed: (i) *R. episcopus* and *R. m. topali* and (ii) *R. siamensis*, *R. cf. siamensis*, *R. huananus*, *R. e. caldwelli*, and *R. cf. macrotis* Phia Oac. *Rhinolophus cf. macrotis* is intermediate between these two groups.

In the dentition, the lower middle (P_3) premolar of our specimens of the three morphological forms of *R. macrotis* s.l. (*R. cf. macrotis*, *R. cf. siamensis*, and *R. cf. macrotis* Phia Oac) is situated in or half-displaced from the toothrow and the lower anterior and posterior premolars (P_2 and P_4) are clearly separated (Figure 3). These characters were also reported for the holotype of *R. m. caldwelli* and *R. huananus* (Allen, 1923; Wu et al., 2008). Likewise, P_3 in *R. macrotis macrotis*, *R. m. topali*, and *R. m. episcopus* is reduced, and its tip does not reach the cingulum of the lower anterior and posterior premolars (P_2 and P_4). Because this tooth is extruded from the toothrow, P_2 and P_4 are in contact (Allen, 1923; Bates & Harrison, 1997; Csorba & Bates, 1995).

Of the three phenetic forms of *R. macrotis* recognized by Sun et al. (2008) in China, the morphological measurements of the small and intermediate forms of Chinese *R. macrotis* match those of our *R. cf. siamensis* and *R. cf. macrotis*, respectively, suggesting they can be treated as the same morphological taxa (hereafter *R. cf. siamensis* and *R. cf. macrotis*). The large form of *R. macrotis* in Jiangxi, China (Sun et al., 2008), agrees more closely with *R. cf. macrotis* Phia Oac, although we found certain differences, for example, ear length = 23–24 mm vs. 29–32 mm and sella height = 5.48 ± 0.31 mm vs. 6.2–6.7 mm, respectively.

3.2 | Glans penis and bacular morphology

The glans penis (one specimen per form) and bacula (two specimens per form) were examined for the three morphological forms of *R. macrotis* s.l. in Vietnam (Figures 5 and 6).

Glans penis: The glans penises of the three morphological forms of *R. macrotis* in Vietnam are readily distinguishable by their size and shape (Figure 5). In *R. cf. macrotis* (Figure 5a), the glans penis is cylindrical (ca. 4 mm in length) and separated from the terminal shaft by a visible fold. The ventral surface is oblong, its dorsal aspect is flattened, and the urinary meatus appears as a long and narrow ridge at the middle of the ventral side. In *R. cf. siamensis* (Figure 5b), the glans penis is bulbous (ca. 3 mm in length) and is also separated from the terminal shaft by a visible boundary and the urinary meatus appears as a long and wide vertical slit, bounded on either side by two small labia-like projections. In *R. cf. macrotis* Phia Oac (Figure 5c), the glans penis is club-shaped (ca. >4 mm in length), the boundary between the glans and shaft is invisible, and the urinary meatus appears as a long and deep vertical slit. Because intraspecific variation in glans penis within each form of Vietnamese *R. macrotis* s.l. was not examined, further investigations are needed to confirm the above observations.

Baculum: In general terms, the baculum of *R. macrotis* s.l. has a slightly compressed dorsoventral basal cone, and dorsal and ventral emarginations on the corresponding proximal margins are slight and wide. The shaft of the baculum has a thickening at the midpoint, which is visible laterally and dorsally. This has a very slight dorsal bend near the base cone, which is more pronounced immediately beyond the thickening. The tip is narrowly rounded off, with a lateral widening and an elongated dorsal knob (Figure 6) (Topál, 1975). However, considerable differences occur in the size and shape of

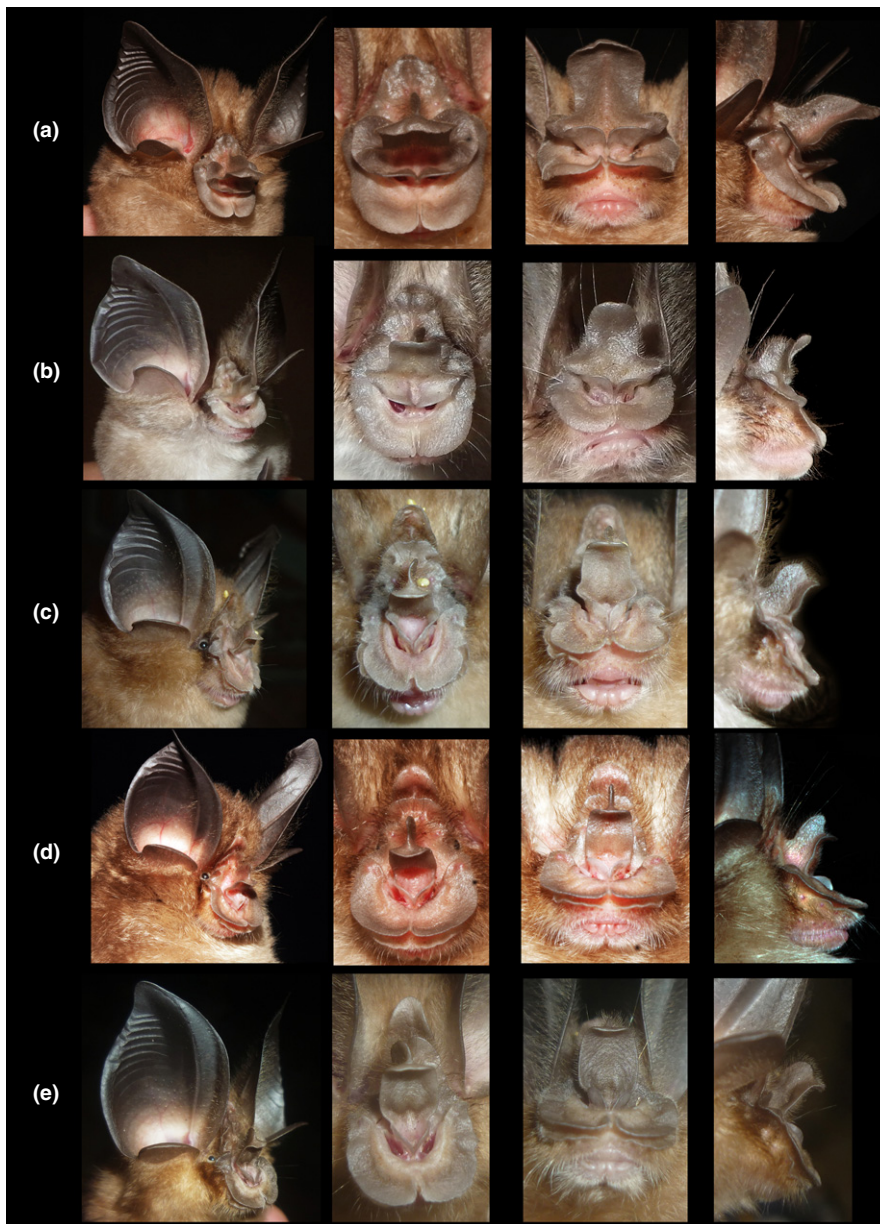


FIGURE 2 Portrait and noseleaf morphology of studied species of the *philippinensis* group collected in Vietnam. a—*R. paradoxolophus* (NH2016-66, ♂); b—*R. marshalli* (IEBR.VN14-0212, ♂); c—*R. cf. macrotis* (IEBR.VN11-0261, ♂); d—*R. cf. siamensis* (IEBR.M-5353, ♂); e—*R. cf. macrotis* Phia Oac (IEBR - VTTu15.0028, ♂). Not to scale

bacula among the three morphological forms of *R. macrotis* s.l. in Vietnam (Figure 6; Table 3). For instance, the baculum of *R. cf. siamensis* (Figure 6c, d) is distinctly smaller in most respects than that of *R. cf. macrotis* and *R. cf. macrotis* Phia Oac (Figure 6a, b and e, f, respectively), whereas those of the latter taxa are nearly identical.

3.3 | Echolocation calls

Echolocation call parameters of our *R. paradoxolophus*, *R. cf. macrotis*, *R. cf. siamensis*, and *R. cf. macrotis* Phia Oac were compared with published data for *R. macrotis*, *R. marshalli*, *R. paradoxolophus*, and *R. rex* from Vietnam and adjacent territories (Table 4). Significant differences were found in echolocation call parameters between these taxa, and body size (expressed by FA) and FmaxE were negatively correlated in general (Figure 7; Table 4). For instance, *R. rex* and *R. paradoxolophus* are large bodied and consequently emit calls with

the lowest FmaxE values (26.8 ± 0.2 kHz and 28.5 ± 0.4 kHz, respectively). Similarly, the FmaxE of the smallest taxon, *R. cf. siamensis* from northern Vietnam and the small form of *R. macrotis* s.l. in southern China (Jiangxi and Guangxi), was the highest recorded (64.7 ± 0.3 kHz to 69.0 ± 0.7 kHz). Between these two extremes, *R. cf. macrotis* Phia Oac bats and those of the large form of *R. macrotis* s.l. in Jiangxi (Sun et al., 2008) overlapped in body size (FA: >45 mm), while their FmaxE ranged from 43.2 kHz (former taxon) to >47.9 kHz (latter taxon). Bats of Vietnamese *R. cf. macrotis* and those of the intermediate form of *R. macrotis* s.l. in Yunnan (Sun et al., 2008) are similar in body size (FA: 42–45 mm) and emit calls with a range of FmaxE from 52.0 kHz (first taxon) to >56.4 kHz (latter taxon). One exception to the negative correlation between body size and FmaxE was found in *R. marshalli*. This species is significantly smaller than *R. cf. macrotis* Phia Oac but emits calls with a similar FmaxE (Figure 7; Table 4).

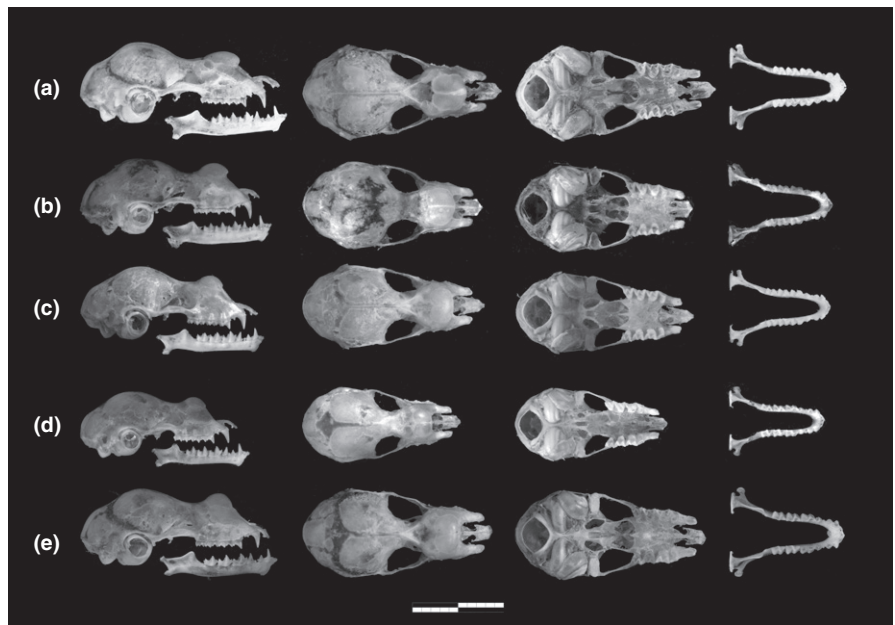


FIGURE 3 Skull photographs of studied species of the *philippinensis* group collected in Vietnam. a—*R. paradoxolophus* (IEBR.VTTu15.006, ♂); b—*R. marshalli* (IEBR.XS15.20, ♂); c—*R. cf. macrotis* (IEBR.VN11-0261, ♂); d—*R. cf. siamensis* (IEBR.VN11-0138, ♂); e—*R. cf. macrotis* Phia Oac (IEBR.VTTu15.0028, ♂). Scale = 10 mm

3.4 | Phylogeographic analyses

3.4.1 | Cytb sequences

The Bayesian tree reconstructed from the *Cytb* alignment is presented in Figure 8. The *philippinensis* group and *R. marshalli* are monophyletic (PP = 1), but within the *philippinensis* group, *R. macrotis* appears to be polyphyletic with four divergent clades. *Rhinolophus marshalli*, *R. rex*, and *R. paradoxolophus* are situated between the clades of *R. macrotis*, although these deep relationships are not robust (PP < 0.7). Clade 1 included bats of the large form of *R. macrotis* s.l. in Jiangxi (Sun et al., 2008) and Jingmen, China (Guo et al., 2013), and occupied a basal position. Clade 2 included only bats of *R. cf. macrotis* Phia Oac and one specimen from Guizhou, southern China (Zhang, Sun, & Feng, 2015). Our specimens of *R. cf. macrotis* and *R. cf. siamensis* grouped together with the small and intermediate forms of *R. macrotis* s.l. from southern China (Sun et al., 2008) and comprised Clade 3. A single Nepalese specimen of *R. macrotis* (or Clade Nepal) was sister to a group uniting bats in Clade 2 and Clade 3 (PP = 1), but the deep sister relationship among them was not robust (PP < 0.5). Likewise, two pairs of taxa including (i) *R. rex* in southern China/*R. paradoxolophus* in northern Vietnam, and (ii) *R. cf. macrotis* (including *R. macrotis* s.l. intermediate form in Yunnan sensu Sun et al., 2008)/*R. cf. siamensis* (including *R. macrotis* s.l. small form in south China sensu Sun et al., 2008), were paraphyletic (Figure 8).

Pairwise nucleotide p-distances estimated from *Cytb* sequences between nominate taxa within the “*R. philippinensis*” group lay between 3.0% and 5.5%, except for *R. rex* and *R. paradoxolophus*, which show low divergence, similar to their intraspecific variation (0.2%–1.1%). These values are significantly smaller than interspecific variation between other *Rhinolophus* taxa such as *R. pusillus* and *R. pearsonii* (>6.8%). Within *R. macrotis* s.l., the Nepalese specimen differed from other bats in clades 1–3 by 3.2%–4.1%, whereas

genetic divergences between and within clades 1–3 were 2.4%–4.1% and <2%, respectively. Thus, genetic distances between the four identified clades of *R. macrotis* are comparable with interspecific variations between nominate taxa within the *philippinensis* group. It should also be noted that *R. cf. siamensis* and *R. cf. macrotis* in Indochina and southern China in Clade 3 are discriminable morphologically and acoustically, but their *Cytb* sequences are identical or only slightly different (Table 5).

3.4.2 | COI sequences

Contrary to the *Cytb* analysis, no *COI* sequences were available for samples of *R. macrotis* s.l. from Nepal and Jiangxi (China) (C7 within Clade 1 in *Cytb* tree; Figure 8). The phylogenetic patterns of taxa in the *COI* tree are comparable with those in the *Cytb* tree, except that two specimens of *R. paradoxolophus* from Khammouane (Laos) appear as sister to the clade containing *R. rex* and *R. paradoxolophus* in northern Laos, Vietnam, and southern China (PP = 0.8) (Figure 9). The *philippinensis* group is also monophyletic, but with relatively low robustness (PP = 0.6). *Rhinolophus marshalli*, *R. rex*, and *R. paradoxolophus* also appear as sister to *R. macrotis* s.l., although their deep sister relationships are not robust (PP < 0.7). The two sister clades of *R. macrotis* s.l. (clades 2 and 3) have maximum robustness (PP = 1).

P-distances calculated from *COI* sequences between different taxa are similar to those calculated from *Cytb* sequences. For instance, interspecific genetic distances within the *philippinensis* group range from 2.4% to 4.6%, except between *R. rex* and *R. paradoxolophus* (0%–2.3%), which is also smaller than distances among other *Rhinolophus* spp. (>9.1%) (Table 5). If *R. paradoxolophus* specimens from northern Laos and northern Vietnam (northern Indochina) and from Khammouane (Laos, central Indochina) are treated as two separate lineages, namely *R. paradoxolophus* 1 and

TABLE 1 External and craniodental measurements (in mm) of *R. macrotis* complex, *R. marshalli*, and *R. paradoxolophus*. Values are given as mean \pm SD (n), min–max. Acronyms and definitions for measurements are given in the text

Characters		<i>R. macrotis</i> —complex										<i>R. marshalli</i>		<i>R. paradoxolophus</i>			
		Subspecies of <i>R. macrotis</i> described in mainland Asia*					Vietnam					Vietnam		Vietnam			
Wt (g)		<i>macrotis</i> ¹	<i>siamensis</i> ²	<i>episcopus</i> ³	<i>caldwelli</i> ⁴	<i>topali</i> ⁵	<i>huananus</i> ⁶	<i>cf. macrotis</i>	<i>cf. siamensis</i>	Phia Oac							
FA	42.79, –	36.1, –	47.5 (45.80–48.96)	43.0	–	45.4 \pm 0.7 (5)	40.8 \pm 1.1 (6)	43.3 \pm 1.2 (5)	39.4 \pm 1.1 (21)	48.6 \pm 1.0 (3)	8.0 (1)	6.5 \pm 1.5 (3)	6.5 \pm 1.5 (3)	8.6 \pm 0.6 (4)	8.0–10.0	54.1 \pm 1.4 (9)	
Tail	21.34	13.0, –	24.0 (19.06–22.29)	–	–	19.0 \pm 1.2 (5)	18.6 \pm 3.2 (6)	19.5 \pm 1.5 (5)	19.1 \pm 1.7 (21)	22.7 \pm 0.5 (3)	–	20.4 \pm 2.0 (5)	20.4 \pm 2.0 (5)	25.9 \pm 1.7 (9)	–	22.7–28.0	25.9 \pm 1.7 (9)
E	21.90	18.9, –	26.0	–	–	23.6 \pm 0.7 (5)	21.3 \pm 1.1 (6)	23.0 \pm 1.3 (5)	20.3 \pm 1.6 (21)	30.7 \pm 1.8 (3)	–	25.4 \pm 1.1 (5)	25.4 \pm 1.1 (5)	31.7 \pm 1.6 (6)	–	29.3–33.1	31.7 \pm 1.6 (6)
Tib	18.0	–	–	17.0	–	–	–	18.2 \pm 0.5 (4)	16.7 \pm 0.5 (19)	19.8 \pm 0.8 (3)	–	19.0 \pm 0.6 (5)	19.0 \pm 0.6 (5)	22.8 \pm 0.7 (9)	–	21.2–23.5	22.8 \pm 0.7 (9)
HF	10.0	–	–	9.0	–	–	–	8.7 \pm 0.2 (4)	7.3 \pm 0.4 (21)	8.8 \pm 0.3 (3)	–	7.7 \pm 0.3 (5)	7.7 \pm 0.3 (5)	9.4 \pm 0.3 (9)	–	9.0–9.9	9.4 \pm 0.3 (9)
HSW	7.57	–	(7.57–8.44)	–	–	9.2 \pm 0.4 (4)	6.8 \pm 0.7 (5)	8.4 \pm 0.1 (4)	7.5 \pm 0.5 (18)	9.5 \pm 0.0 (3)	–	8.0 \pm 0.5 (5)	8.0 \pm 0.5 (5)	11.6 \pm 0.6 (6)	–	10.7–12.2	11.6 \pm 0.6 (6)
SEH	–	–	(4.13–5.93)	–	–	–	–	8.2–8.5	6.5–8.3	9.5–9.5	–	7.4–8.7	7.4–8.7	–	–	–	–
SEW	–	–	(3.05–3.78)	–	–	–	–	–	3.9 \pm 0.4 (15)	6.4 \pm 0.3 (3)	–	5.2 \pm 0.4 (4)	5.2 \pm 0.4 (4)	–	–	–	–
3 rd mt	30.50	34.5	–	31.5	–	32.1 \pm 0.5 (4)	29.8 \pm 0.5 (5)	31.7 \pm 0.4 (4)	29.4 \pm 0.9 (19)	36.4 \pm 0.3 (3)	–	33.3 \pm 0.4 (5)	33.3 \pm 0.4 (5)	40.1 \pm 1.1 (9)	–	37.9–41.8	40.1 \pm 1.1 (9)
4 th mt	31.71	36.0	–	33.0	–	31.5–32.6	29.2–30.4	31.3–32.2	27.9–31.1	36.2–36.7	–	32.6–33.5	32.6–33.5	–	–	–	–
5 th mt	31.93	36.0	–	33.0	–	32.8 \pm 0.7 (4)	30.9 \pm 0.4 (5)	33.2 \pm 0.7 (4)	30.7 \pm 1.1 (19)	37.5 \pm 0.3 (3)	–	34.5 \pm 0.9 (5)	34.5 \pm 0.9 (5)	42.2 \pm 1.0 (9)	–	39.7–43.2	42.2 \pm 1.0 (9)
SL	17.78	15.4, 15.3	19.0 (18.23–19.22)	18.0	–	18.16 \pm 0.11 (5)	16.51 \pm 0.23 (5)	18.10 \pm 0.08 (3)	16.14 \pm 0.37 (20)	19.57 \pm 0.04 (3)	–	18.24 \pm 0.20 (4)	18.24 \pm 0.20 (4)	20.77 \pm 0.32 (9)	–	20.32–21.31	20.77 \pm 0.32 (9)
CCL	17.0	–	–	15.5	–	–	–	16.03 \pm 0.04 (3)	14.22 \pm 0.37 (20)	17.39 \pm 0.03 (3)	–	16.03 \pm 0.16 (4)	16.03 \pm 0.16 (4)	18.56 \pm 0.31 (9)	–	17.97–19.11	18.56 \pm 0.31 (9)
ZB	8.14	6.9, 7.1	8.2 (7.99–8.94)	7.8	–	8.22 \pm 0.08 (5)	7.70 \pm 0.02 (5)	7.99 \pm 0.16 (3)	7.42 \pm 0.19 (20)	8.74 \pm 0.10 (3)	–	8.31 \pm 0.14 (4)	8.31 \pm 0.14 (4)	9.34 \pm 0.20 (9)	–	9.15–9.74	9.34 \pm 0.20 (9)

(Continues)

TABLE 1 (Continued)

Characters		R. macrotis-complex										R. paradoxolophus											
		Subspecies of R. macrotis described in mainland Asia*										Vietnam		Vietnam									
		macrotis ¹		siamensis ²		episcopopus ³		calldwelli ⁴		topali ⁵		huanamu ⁶		cf. macrotis		cf. siamensis		Phia Oac		R. marshalli		R. paradoxolophus	
MB	8.66	7.4, 7.2	9.2	8.5	8.80 ± 0.07 (5)	8.24 ± 0.08 (5)	8.62 ± 0.01 (3)	8.00 ± 0.21 (20)	9.44 ± 0.14 (3)	9.07 ± 0.09 (4)	10.37 ± 0.10 (9)	8.70–8.90	8.18–8.36	8.61–8.63	7.51–8.40	9.29–9.57	5.48 ± 0.09 (3)	4.85 ± 0.09 (4)	8.96–9.17	10.15–10.49	4.73–4.93	5.91 ± 0.23 (9)	5.57–6.31
ALSW	3.7, 3.6				–	–	4.96 ± 0.08 (3)	4.01–4.41	5.37–5.54	4.85 ± 0.09 (4)	5.91 ± 0.23 (9)			4.87–5.02	4.01–4.41	5.37–5.54	4.73–4.93	8.96–9.17	10.15–10.49	4.73–4.93	5.91 ± 0.23 (9)	5.57–6.31	
AMSW					–	–	3.51 ± 0.06 (3)	2.97 ± 0.15 (20)	3.98 ± 0.06 (3)	3.54 ± 0.03 (4)	4.08 ± 0.07 (9)			3.44–3.56	2.71–3.24	3.91–4.01	3.50–3.58	8.96–9.17	10.15–10.49	4.73–4.93	5.91 ± 0.23 (9)	5.57–6.31	
C ¹ C ¹	3.85	4.4 (3.59–4.13)	3.8*	3.0	4.08 ± 0.04 (5)	3.40 ± 0.16 (6)	3.82 ± 0.05 (3)	3.34 ± 0.16 (20)	4.04 ± 0.05 (3)	3.73 ± 0.08 (4)	4.22 ± 0.12 (9)	4.00–4.10	3.11–3.55	3.78–3.87	3.03–3.60	4.00–4.09	4.00–4.09	3.65–3.82	3.98–4.39	3.65–3.82	3.98–4.39	3.98–4.39	3.98–4.39
M ³ M ³	5.77	4.8, 4.7	6.2 (5.81–6.17)	5.7	6.06 ± 0.09 (5)	5.24 ± 0.13 (6)	5.73 ± 0.06 (3)	5.23 ± 0.17 (20)	6.20 ± 0.09 (3)	5.51 ± 0.06 (4)	6.48 ± 0.15 (9)	5.95–6.21	5.03–5.40	5.66–5.77	4.97–5.60	6.12–6.30	6.12–6.30	5.47–5.59	6.30–6.67	5.47–5.59	6.30–6.67	6.30–6.67	6.30–6.67
PL	3.68	–	3.7	3.0	3.62 ± 0.07 (4)	3.16 ± 0.13 (6)	3.35 ± 0.09 (3)	3.11 ± 0.26 (20)	4.09 ± 0.15 (3)	3.58 ± 0.27 (4)	4.26 ± 0.21 (9)	3.56–3.72	2.95–3.28	3.29–3.45	2.31–3.45	3.97–4.25	3.97–4.25	3.29–3.87	3.95–4.51	3.29–3.87	3.95–4.51	3.95–4.51	3.95–4.51
IC	2.40	–	–	–	2.43 ± 0.17 (5)	2.37 ± 0.08 (5)	2.31 ± 0.05 (3)	2.23 ± 0.06 (20)	2.60 ± 0.01 (3)	2.38 ± 0.03 (4)	2.79 ± 0.12 (9)	2.17–2.63	2.26–2.47	2.26–2.35	2.08–2.36	2.59–2.61	2.59–2.61	2.35–2.41	2.62–2.97	2.35–2.41	2.62–2.97	2.62–2.97	2.62–2.97
CM ³	6.44	5.3, 5.2	7.0 (6.43–7.10)	6.0	6.62 ± 0.08 (5)	5.89 ± 0.07 (6)	6.50 ± 0.09 (3)	5.75 ± 0.17 (20)	7.17 ± 0.04 (3)	6.32 ± 0.15 (4)	7.56 ± 0.15 (9)	6.50–6.70	5.80–5.96	6.42–6.60	5.51–6.04	7.12–7.20	7.12–7.20	6.15–6.52	7.27–7.73	6.15–6.52	7.27–7.73	7.27–7.73	7.27–7.73
ML	11.19	9.5, 9.3*	12	11.4	11.72 ± 0.20 (5)	10.24 ± 0.22 (5)	11.39 ± 0.08 (3)	10.22 ± 0.30 (20)	12.53 ± 0.07 (3)	11.41 ± 0.19 (4)	13.48 ± 0.23 (9)	11.50–11.90	9.95–10.47	11.30–11.45	9.68–10.80	12.45–12.59	12.45–12.59	11.21–11.59	13.27–14.02	11.21–11.59	13.27–14.02	13.27–14.02	13.27–14.02
CM ₃	6.64	5.6, 5.7	7.2	6.5	6.84 ± 0.05 (5)	6.03 ± 0.14 (5)	6.65 ± 0.03 (3)	5.96 ± 0.18 (20)	7.34 ± 0.09 (3)	6.61 ± 0.18 (4)	7.70 ± 0.11 (9)	6.80–6.90	5.81–6.15	6.61–6.67	5.70–6.24	7.24–7.41	7.24–7.41	6.41–6.85	7.52–7.89	6.41–6.85	7.52–7.89	7.52–7.89	7.52–7.89

Sources: ¹—mean values of holotype and five addition specimens collected in northeastern India (Csorba & Bates, 1995); ²—holotype and paratype (Gyldenstolpe, 1917); ³—holotype (Allen, 1923) and topotypes in parentheses (Wu et al., 2008); ⁴—holotype (Allen, 1923), *—measurements taken from the skull photograph; ⁵—type series (Csorba & Bates, 1995); ⁶—type series (Wu et al., 2008).

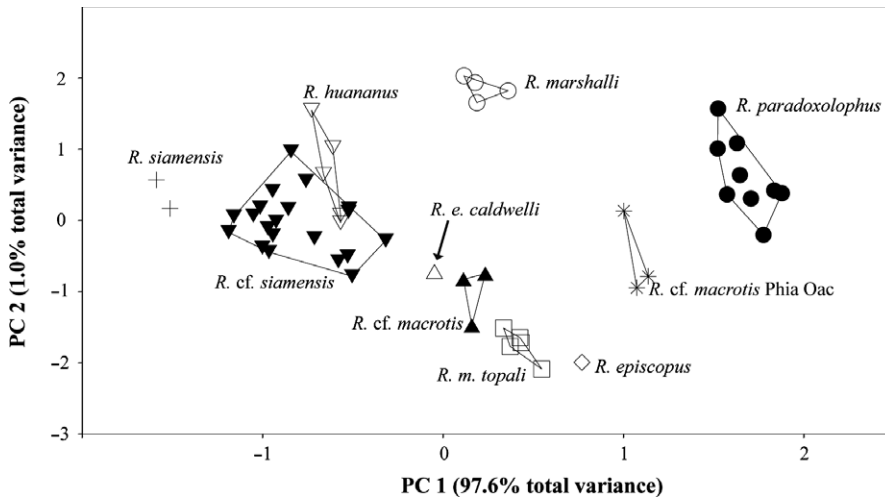


FIGURE 4 Principal components analysis (PCA) on seven craniodental characters of *Rhinolophus* spp

TABLE 2 Factor loading for PCs obtained from PCA of seven cranial characters

Characters	PC 1	PC 2
SL	0.37	0.11
ZB	0.33	0.41
MB	0.37	0.55
CM3	0.41	-0.19
M3M3	0.34	-0.67
ML	0.42	-0.01
CM3	0.39	-0.17
Eigenvalue	0.0136	0.0001
% variance	97.6	1.00

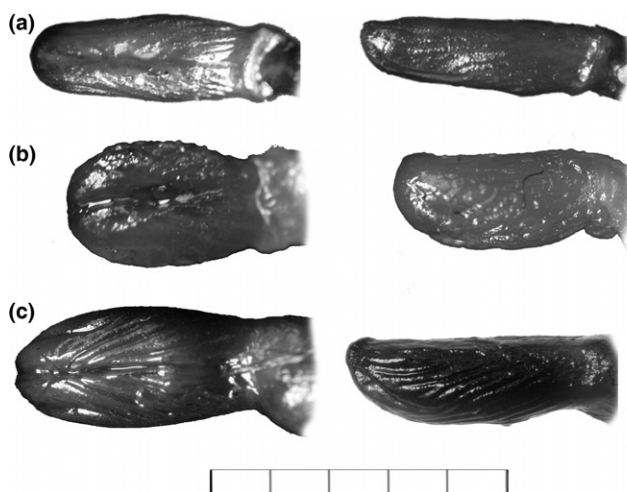


FIGURE 5 Morphology of the glans penis of three morphological forms of *R. macrotis* s.l. recorded in Vietnam. From left to right (ventral view and lateral view): a—*R. cf. macrotis* (IEBR.VN11-0201); b—*R. cf. siamensis* (IEBR.VN11-0138); and c—*R. cf. macrotis* Phia Oac (IEBR.POPD16.20). Scale = 5 mm

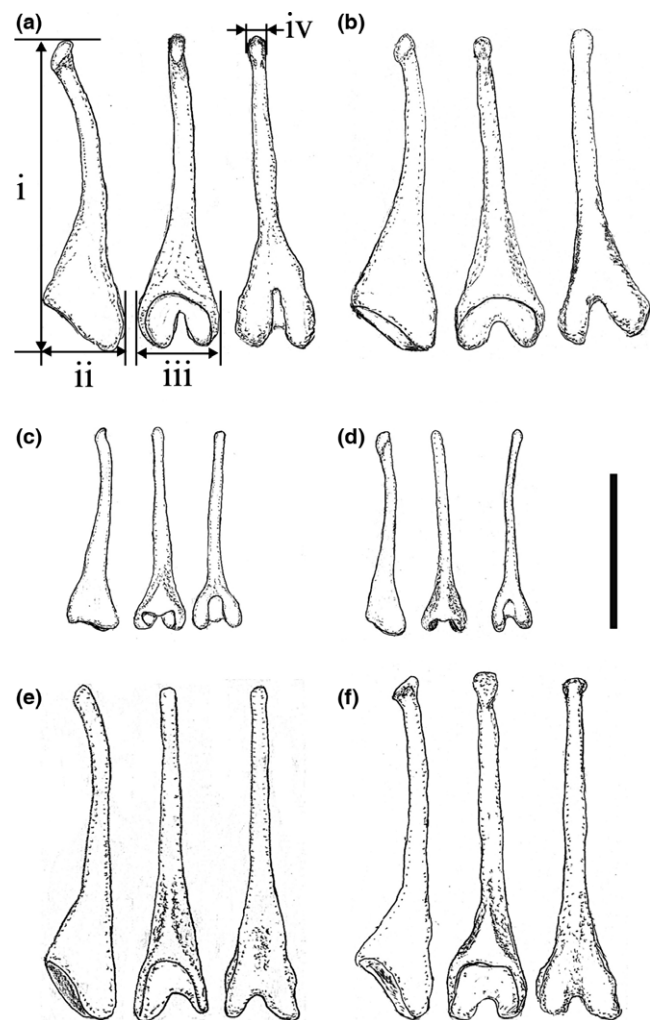


FIGURE 6 Bacula of specimens of different taxa within *R. macrotis* s.l. collected in Vietnam. From left to right (lateral, dorsal, and ventral view): *R. cf. macrotis* (Vietnam: a—IEBR.VN11-0082; b—IEBR.VN11-0201); *R. cf. siamensis* (Vietnam: c—IEBR.VN11-0138; d—IEBR.POPD16.24); and *R. cf. macrotis* Phia Oac (Vietnam: e—IEBR.VTTu15.0027; f—IEBR.POPD16.20). Measurements as in Table 3: i—total length; ii—height of basal cone; iii—width of basal cone; and iv—width of tip. Scale = 2 mm

TABLE 3 Measurements (in mm) of extracted baculum of Vietnamese *Rhinolophus macrotis* s.l.

Taxon	Total length	Width of basal cone	Height of basal cone	Width of tip
<i>R. cf. macrotis</i> (A, B)	4.05, 4.11	1.05, 1.15	1.04, 1.10	0.26, 0.28
<i>R. cf. siamensis</i> (C, D)	2.62, 2.61	0.66, 0.57	0.67, 0.51	0.15, 0.14
<i>R. cf. macrotis</i> Phia Oac (E, F)	4.31, 4.44	0.98, 1.01	0.91, 0.99	0.22, 0.31

R. paradoxolophus 2, respectively, genetic distances between the two lineages are significantly higher than those within each lineage (2.1%–2.8% vs. <1.4%, respectively). Within *R. macrotis* s.l., p-distances among bats in clades 2 and 3 ranged from 1.7% to 2.7%, higher than those within each clade (<1.4%), whereas interspecific genetic distances between *R. cf. macrotis* and *R. cf. siamensis* in Vietnam and nearby regions ranged from 0.2% to 1.1% (Table 5).

3.4.3 | Identification key for five morphological taxa belonging to the *philippinensis* group in Vietnam

1a. Supplementary leaflet absent; sella with conspicuous basal lappets; lancet greatly reduced. Internarial cup expanded sideways to form prominent leaflets. Sella very long, leaf-like, approaching ears in length. Connecting process with very wide

base (Figure 2a and b). Anterior median swellings low, long, and well-expanded anteriorly beyond the front of the rostral wall (Figure 3a and b).2
 1b. Supplementary leaflet clearly visible; sella without basal lappets (Figure 2c–e); lancet long, lateral margins convex with a rounded tip; connecting process high, lower part almost parallel with sella; anterior median swellings well inflated, long, and expanded anteriorly but reach slightly beyond front of rostral wall (Figure 3c–e).3
 2a. Size larger: FA > 50 mm; ear enormous, length >29 mm; lancet broadly rounded; margins of internarial cup passing beneath base of sella; SL > 20 mm; ML > 13 mm *R. paradoxolophus*
 2b. Size smaller: FA < 47 mm; ear enormous, length 23–27 mm; lancet more or less triangular; lateral margins of internarial cup merge with margins of sella; SL < 19 mm; ML < 12 mm. *R. marshalli*

TABLE 4 Call parameters (mean ± SD) of different species of the *philippinensis* group recorded in northeastern Vietnam and south China

Taxon	FA (mm)	n	SF (kHz)	EF (kHz)	FmaxE (kHz)	D (ms)	IPI (ms)
<i>R. macrotis</i> "Phia Oac" (Male)	48.6 ± 1.0	1	37.7 ± 0.5	37.3 ± 0.9	43.2 ± 0.0	31.6 ± 5.5	66.8 ± 24.1
<i>R. macrotis</i> large form Jiangxi ¹							
Male	48	1	–	–	47.9 ± 0.2	–	–
Female	45.2 ± 3.7	9	–	–	49.3 ± 0.3	–	–
<i>R. cf. macrotis</i> (NW Vietnam)*	43.3 ± 1.2	1	44.8 ± 1.2	48.0 ± 1.6	52.0 ± 0.3	31.4 ± 2.4	80.1 ± 15.5
<i>R. cf. macrotis</i> (=intermediate form) Yunnan ¹							
Male	43.5 ± 0.5	3	–	–	56.4 ± 0.3	–	–
Female	42.3 ± 0.8	6	–	–	57.7 ± 0.3	–	–
<i>R. cf. siamensis</i> (NE Vietnam) [†]	40.2 ± 0.9	3	59.4 ± 1.2	53.1 ± 2.4	66.4 ± 0.9	30.4 ± 7.5	56.3 ± 22.8
<i>R. cf. siamensis</i> (NW Vietnam) [†]	39.2 ± 0.8	3	61.6 ± 2.9	61.1 ± 2.1	69.0 ± 0.7	43.8 ± 9.5	102.9 ± 27
<i>R. cf. siamensis</i> (=small form) Guangxi ¹							
Male	39.8 ± 0.5	4	–	–	66.1 ± 0.2	–	–
Female	39.0, 40.5	2	–	–	67.3 ± 0.3	–	–
<i>R. cf. siamensis</i> (=small form) Jiangxi ¹ (Female)	39.5, 40.0	2	–	–	64.7 ± 0.3	–	–
<i>R. paradoxolophus</i> NE Vietnam*	54.1 ± 1.4*	2	23.5 ± 0.7	21.5 ± 2.1	28.3 ± 0.4	67.5 ± 3.5	85 ± 21.2
<i>R. paradoxolophus</i> NE Vietnam ²		44	23.7 ± 1.0	22.7 ± 1.3	28.5 ± 0.4	60.5 ± 12.4	108.1 ± 21.5
<i>R. rex</i> Guizhou, China ³	54.1 ± 1.4	18			26.8 ± 0.2		
<i>R. marshalli</i> Vietnam ⁴	45.0 ± 0.6*	1	43.5–44	42.3–44	44	44.9	–
<i>R. marshalli</i> Guangxi ⁵							
Male	43.75 ± 2.43	9	–	–	43.30 ± 0.55	–	–
Female	42.06 ± 2.46	8	–	–	44.47 ± 0.63	–	–

Sources: *recent study; n—number of individual examined acoustically; ¹Sun et al., 2008; ²Furey, Mackie, & Racey, 2009; ³Feng et al., 2001; ⁴Thong et al., 2007; and ⁵Liu, Jiang, Berquist, & Feng, 2009.

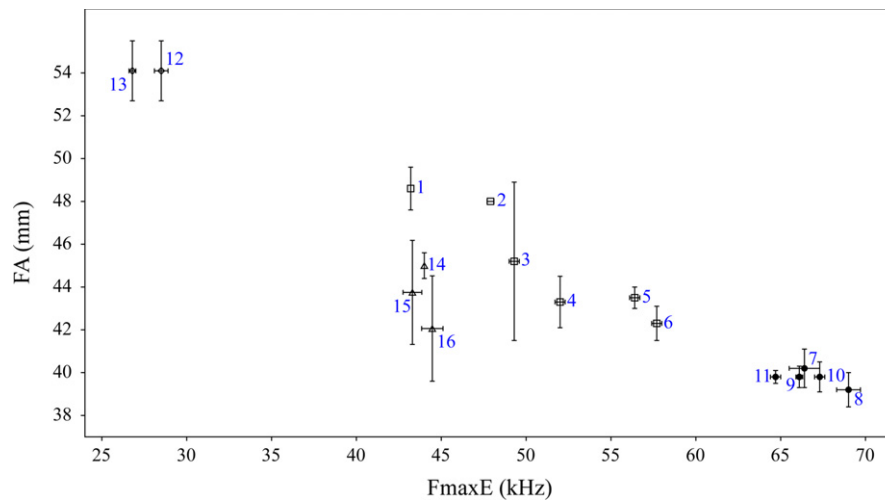


FIGURE 7 Relationships between forearm length (FA) ($x \pm SD$) and frequency of maximum energy (FmaxE) ($x \pm SD$) in *Rhinolophus* spp. within the *philippinensis* group. 1—*R. cf. macrotis* Phia Oac (male); 2—*R. cf. macrotis* Jiangxi (male); 3—*R. cf. macrotis* Jiangxi (female); 4—*R. cf. macrotis* NW Vietnam; 5—*R. cf. macrotis* Yunnan (male); 6—*R. cf. macrotis* Yunnan (female); 7—*R. cf. siamensis* NE Vietnam; 8—*R. cf. siamensis* NW Vietnam; 9—*R. cf. siamensis* Guangxi (male); 10—*R. cf. siamensis* Guangxi (female); 11—*R. cf. siamensis* Jiangxi (female); 12—*R. paradoxolophus* NE Vietnam; 13—*R. rex* Guizhou, China; 14—*R. marshalli* NE Vietnam; 15—*R. marshalli* Guangxi (male); and 16—*R. marshalli* Guangxi (female)

3a. Size large: FA > 47 mm; ear enormous, length >29 mm; sella parallel-sided, width >4 mm, but gradually narrowing toward base; SL > 19 mm; ML > 12 mm; interpterygoid shallow and cone-shaped. *R. cf. macrotis* Phia Oac

3b. Size medium: FA 42–45 mm; ear large, length >23 mm; sella parallel-sided, width <3 mm, but significantly broader at base; SL <18–19 mm; ML 11–12 mm; interpterygoid shallow and cone-shaped. *R. cf. macrotis*

3c. Size small: FA < 42 mm; ear large, length usually <23 mm; sella parallel-sided, width usually <3 mm; SL < 17 mm; ML < 11 mm; interpterygoid deep and narrow. . . . *R. cf. siamensis*

4 | DISCUSSION

4.1 | How many species of the *philippinensis* group occur in Vietnam and nearby regions?

Most early bat taxonomists relied on classical morphological examination of several discrete characters when designating boundaries between species or higher taxa (e.g., Andersen, 1905; Tate, 1943). However, recent investigations have indicated that the convergence in phenotypes is relatively common in many bat taxa, for example, *Myotis* spp. (Ruedi & Mayer, 2001), *Hipposideros* spp. (Douangboubpha et al., 2010; Rakotoarivelo, Willows-Munro, Schoeman, Lamb, & Goodman, 2015; Thong et al., 2012), and *Rhinolophus* spp. (Ith et al., 2015; Jacobs et al., 2013; Taylor et al., 2012). In Asia, many bat species that were previously thought to be widespread are now regarded as cryptic species complexes, and scientific understanding of regional bat diversity is restricted by current taxonomy and gaps in survey coverage (Campbell, Schneider, Adnan, Zubaid, & Kunz, 2004; Francis et al., 2010; Murray et al., 2012).

In the case of the *R. macrotis* complex, different species—although distinguishable by certain morphological differences—have been synonymized under the nominal species, *R. macrotis* (Csorba & Bates, 1995; Tate, 1943). However, two of the seven recognized subspecies of *R. macrotis*, namely *R. hirsutus* and *R. siamensis* (Francis, 2008), have been recently validated as distinct species. In contrast to previous studies, our analyses of morphological traits, echolocation calls, and genetic sequences suggest that *R. macrotis* sensu stricto (s.str.) may be endemic to the Indian subcontinent, whereas bats hitherto allocated to *R. macrotis* s.l. in Vietnam and nearby regions should be classified into different species including the following: (i) *R. macrotis* s.l. (=large form found in Jiangxi and Jingmen, China (Sun et al., 2008; Guo et al., 2013)); (ii) *R. cf. macrotis* Phia Oac; (iii) *R. cf. macrotis* (including *R. macrotis* s.l. = the intermediate form in Yunnan (Sun et al., 2008)); and (iv) *R. cf. siamensis* (including *R. macrotis* s.l. = small form in southern China (Sun et al., 2008)). Further investigations of the acoustic and genetic traits of type or topotype material of recognized subspecies of *R. macrotis* s.l. are needed to determine their affinities with recently recognized cryptic taxa.

Previous studies in Indochina and China identified certain bats as *R. siamensis* following Hendrichsen, Bates, and Hayes (2001), who recognized a small-sized specimen collected in Pu Mat, central Vietnam, as possibly the genuine *R. siamensis*. Other specimens from the region formerly allocated to the nominate taxon were observed to be intermediate in body size between *R. siamensis* and *R. macrotis* (Francis, 2008; Hendrichsen et al., 2001; Kruskop, 2013; Osgood, 1932; Smith et al., 2008). Wu et al. (2008) considered that bats intermediate between *R. siamensis* and *R. macrotis* might belong to a newly described species, *R. huananus*, whereas Zhang et al. (2009) suggested that *R. huananus* may be a synonym of *R. siamensis*. Our

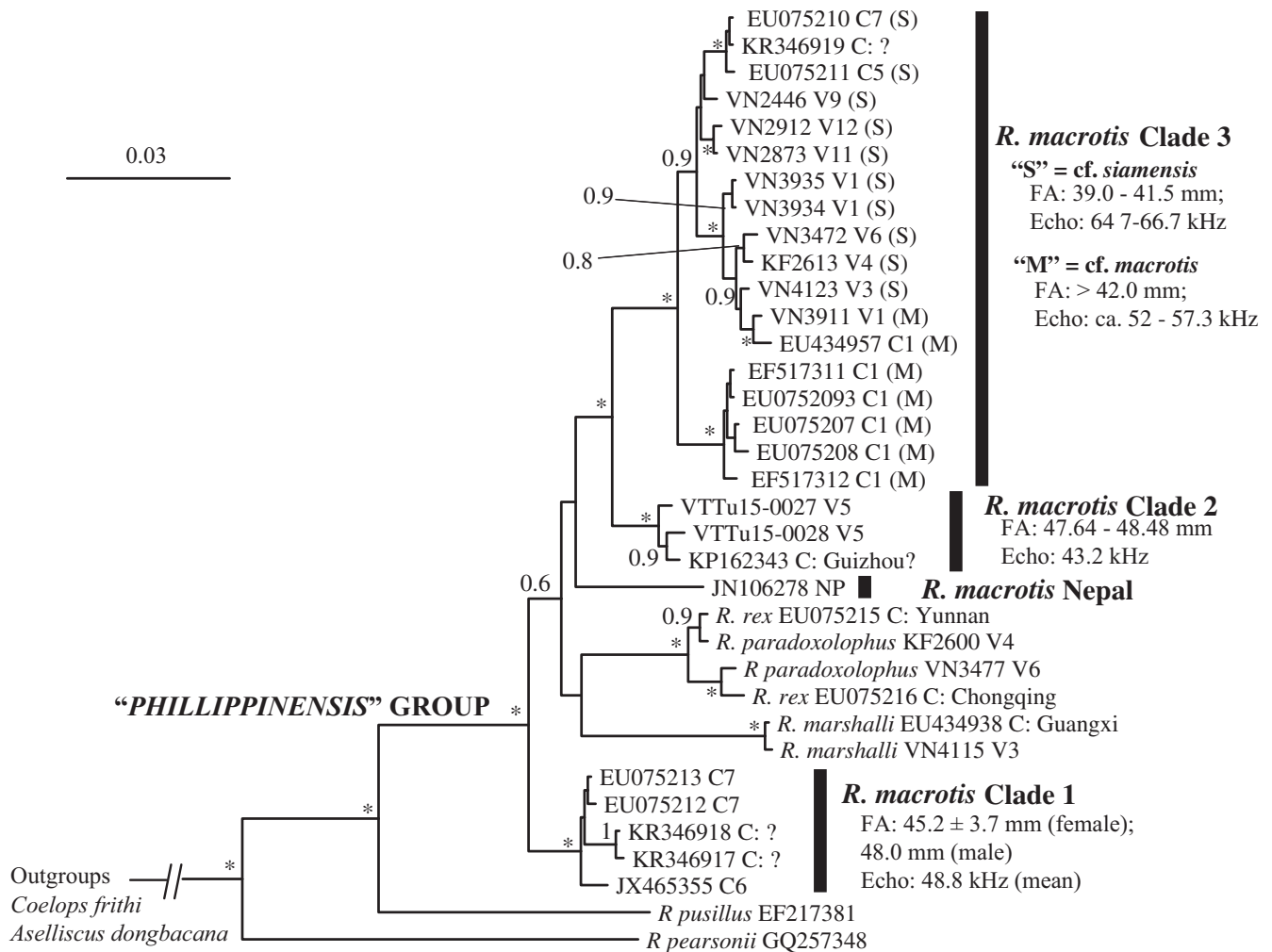


FIGURE 8 Bayesian tree reconstructed from *Cytb* sequences. The numbers on nodes represent posterior probabilities. The asterisk “*” indicates that the node was supported by maximal values of robustness (PP = 1). The localities of specimens examined were illustrated in Figure 1, Appendix 1, and Table S4.

morphological comparison shows that Vietnamese bats of *R. cf. siamensis* overlap with the type material of *R. huananus* in a cluster between the type specimens of *R. siamensis* and *R. e. caldwelli* (Fig. 4). This suggests that bats of *R. cf. siamensis* in this study belong to the same taxon as *R. huananus*. Further studies including acoustic and/or genetic analyses of type or topotype material of genuine *R. siamensis* are needed to confirm this taxonomic inference.

The significant overlap in body size and echolocation call parameters between *R. rex* in China and *R. paradoxolophus* in northern Vietnam supports previous suggestions that these taxa may be conspecific (Csorba et al., 2003; Hill, 1972; Zhang et al., 2009). However, interspecific divergences in DNA barcode sequences (*COI*) between two specimens of *R. paradoxolophus* collected in Khammouane, Laos (or *R. paradoxolophus* 2), and those of the clade uniting Chinese *R. rex* and *R. paradoxolophus* in northern Vietnam (*R. paradoxolophus* 1) were comparable with interspecific distances within the “*macrotis*” complex. Morphological comparisons of *R. paradoxolophus* s.str. in Quang Tri Province (central Vietnam) (which may be conspecific with *R. paradoxolophus* 2 in

Khammouane, Laos, due to their geographic proximity) and those from northern Vietnam reveal that the former is generally larger in body size (Hoang Trung Thanh, pers. obs.). Thus, although the phylogenetic patterns we obtained among matrilineal lineages from distant geographic localities could be indicative of female philopatry (Hassanin et al., 2015; Kerth, Mayer, & König, 2000; Pereira, Salgueiro, Rodrigues, Coelho, & Palmeirim, 2009; Rivers, Butlin, & Altringham, 2005; Tu et al., 2017), further morphological, acoustic, and genetic studies are needed to test whether such genetic divergences represent cryptic diversity.

4.2 | Low genetic divergence between taxa in the philippinensis group

Different species within the *philippinensis* group are readily distinguishable by their morphological and acoustic traits, but levels of mtDNA sequence divergence revealed in this study were significantly lower than those found between other morphological groups within the genus. In particular, mtDNA sequences of pairs of *R. cf.*

TABLE 5 Range (min–max) of uncorrected p-distances (%) between *Rhinolophus* spp., based on Cytb (1,140 bp, below the diagonal) and COI (657 bp, above the diagonal) gene sequences

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13
1	13.5/17.2	17.7–20.1	17.5–19.0	17.2–18.0	16.7–18.8	17.2–18.8	16.7–18.7	NA	NA	17.4–18.3	17.8–19.1	17.8–18.9	18.0–18.9
2	15.3–16.3	9.6/16.1	9.1–14.6	9.9–15.4	9.6–15.9	9.6–15.9	10.7–14.8	NA	NA	9.6–15.2	9.3–16.3	9.3–16.3	9.4–16.0
3	15.4–15.4	7.8–10.1	0.6/0.1	2.6–2.6	2.6–3.4	2.6–3.4	3.0–3.0	NA	NA	2.4–2.7	2.4–3.7	3.0–3.2	2.9–3.3
4	14.7–15.4	7.5–9.9	4.6–5.2	0.0/1.1	0.0–2.3	0.0–1.1	2.3–2.3	NA	NA	3.5–3.5	2.9–4.2	3.3–3.5	3.3–3.5
5	14.6–15.3	7.6–9.8	4.6–5.3	0.2–1.1	0.0–2.8/1.0	NA	NA	NA	NA	3.5–4.0	2.9–4.6	3.5–4.3	3.3–4.6
6	NA	NA	NA	NA	NA	0.0–1.4/–	2.1–2.8	NA	NA	3.5–4.0	3.7–4.6	3.3–4.1	3.3–4.3
7	NA	NA	NA	NA	NA	NA	0.0/–	NA	NA	3.7–3.7	3.6–4.6	4.1–4.3	4.1–4.6
8	15.5–16.0	7.7–10.7	4.9–5.0	4.0–4.5	4.2–4.6	NA	NA	NA	NA	NA	NA	NA	NA
9	15.0–15.5	6.8–9.0	4.4–5.0	3.3–4.0	3.3–4.0	NA	NA	3.3–3.7	–/0.1–1.1	NA	NA	NA	NA
10	14.6–15.3	7.5–9.7	4.6–4.6	3.0–3.4	3.0–3.5	NA	NA	3.2–3.6	2.5–3.3	0.3/0.4–0.5	1.7–2.7	2.4–2.6	2.3–2.7
11	14.7–15.9	7.1–10.1	4.7–5.5	3.6–4.5	3.6–4.5	NA	NA	3.8–4.1	3.0–4.1	2.4–3.1	0–1.4/0.0–2.0	NA	NA
12	14.7–15.9	7.1–10.1	4.8–5.5	3.9–4.5	3.9–4.5	NA	NA	3.8–4.0	3.1–4.1	2.6–3.1	NA	0.8/0.0–2.0	0.2–1.1
13	14.9–15.8	7.3–9.8	4.7–5.5	3.6–4.3	3.6–4.5	NA	NA	3.8–4.1	3.0–3.9	2.4–3.1	NA	0.4–1.8	0.5/0.0–1.1

Taxon: 1—out-groups (*Coelops frithi*; *A. dongbacana*); 2—partial species (*R. pearsonii* and *R. pusillus*); 3—*R. marshalli*; 4—*R. rex*; 5—*R. paradoxolophus*; 6—*R. paradoxolophus* 1; 7—*R. paradoxolophus* 2; 8—*R. macrotis* Nepal; 9—*R. macrotis* Clade 1; 10—*R. macrotis* Clade 2 (*R. macrotis* Phia Oac); 11—*R. macrotis* Clade 3; 12—*R. macrotis* Clade 3 “M=cf. *macrotis*”; and 13—*R. macrotis* Clade 3 “S=cf. *siamensis*”.

NA—not applicable. Values in bold before and after the slashes show intraspecific variation calculated from respective Cytb and COI sequences.

epoch, South-East Asia was a single block of rainforest due to the prevailing warm and humid climatic conditions (Morley, 2000). However, the uplift of Himalayan–Tibetan plateau about 3.6–2.6 Mya and the onset of extensive glaciations in the Northern Hemisphere during the late Pliocene and Pleistocene epochs led to repeated cycles of cool and arid glacial periods and warm and humid interglacial periods in Asia (An, Kutzbach, Prell, & Porter, 2001). Associated with these climatic oscillations, forest expansion and contraction events across the region during Pleistocene may have acted causal factors in shaping current diversity and distribution of Asian biota (Meijaard, 2003; Woodruff, 2010). Because *Rhinolophus* spp. are recognized as forest-interior specialists (Kingston, Francis, Akbar, & Kunz, 2003), contraction and expansion of forests during Plio-Pleistocene have been regarded as major factors driving their biogeographical history (Flanders, Wei, Rossiter, & Zhang, 2011; Mao, He et al., 2013; Mao, Zhu, Zhang, & Rossiter, 2010; Rossiter, Benda, Dietz, Zhang, & Jones, 2007; Tu et al., 2017). For the *R. macrotis* group, we suggest that the vicariance of the most common ancestors of recent taxa might have taken place due to the persistence of different allopatric refugia across the region during Pleistocene glacial periods (Bird, Taylor, & Hunt, 2005; Gathorne-Hardy, Syaukani Davies, Eggleton, & Jones, 2002; Lin et al., 2014; Morgan, Somboon, & Walto, 2013; Tu et al., 2015, 2017). As a consequence, vicariant populations adaptively evolved under different ecological selections imposed by isolated refugia which may have led to shifts in their morphology (noseleaf structure and body, skull, glans penis, and baculum morphology) and echolocation systems, and subsequently their own SMRSs. Depending on the status of SMRSs of each taxon, the restoration of connectivity between some of those during interglacial periods allowed ancient introgression events between some taxa that retained their relatedness (Mao, Zhang et al., 2010; Mao, He et al., 2013; Mao, Thong et al., 2013). However, to test this hypothesis, further investigations including genetic analyses of both mitochondrial and nuclear genomes are needed (Berthier et al., 2006; Hassanin et al., 2015; Mao, Zhang et al., 2010; Nesi et al., 2011; Tu et al., 2017).

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

APPENDIX

APPENDIX 1 Studied specimens of Vietnamese *Rhinolophus* spp

Species	Field N°/Catalogue code	Tissue code	Sex	Year	Locality, Province, Region	Morphological examination E—External C—Craniodental G—Glans penis B—Baculum	FmaxE (KhZ)	Cytb	COI	Morp-form	Clade	GenBank accession N°	
<i>R. macrotis</i>	VN11-0082	VN11-0082	♂	2011	Copia NR, Son La, NW	E, C, B			KY652914	M	3		
<i>R. macrotis</i>	VN11-0089		♂	2011	Copia NR, Son La, NW	E				M			
<i>R. macrotis</i>	VN11-0201	VN11-0201	♂	2011	Copia NR, Son La, NW	E, C, G, B			KY652911	M	3		
<i>R. macrotis</i>	VN11-0261		♂	2011	Copia NR, Son La, NW	E, C				M			
<i>R. macrotis</i>	VN3911B7	VN3911	♀	2014	Hoang Lien NP, Lao Cai, NW	E	52.0	KY652900		M	3		
<i>R. macrotis</i>	B250813.40	VN2873	♂	2013	Bac Huong Hoa NR, Quang Tri, Central	E		KY652901		S	3		
<i>R. macrotis</i>	VN2912B71	VN2912	♂	2013	Dakrong NR, Quang Tri, Central	E		KY652905		S	3		
<i>R. macrotis</i>	VN11-0697	VN11-0697	♀	2011	Phong Nha Ke Bang NP, Quang Binh, Central	E		KY652913		S	3		
<i>R. macrotis</i>	XL 011 a		♀	2012	Xuan Lien NR, Thanh Hoa, Central	E, C				S			
<i>R. macrotis</i>	XL 011 b		♂	2012	Xuan Lien NR, Thanh Hoa, Central	E, C				S			
<i>R. macrotis</i>	XL 012 b		♂	2012	Xuan Lien NR, Thanh Hoa, Central	E, C				S			
<i>R. macrotis</i>	XL 018 a		♀	2012	Xuan Lien NR, Thanh Hoa, Central	E, C				S			
<i>R. macrotis</i>	XL 018 b		♂	2012	Xuan Lien NR, Thanh Hoa, Central	E, C				S			
<i>R. macrotis</i>	XL 03		♀	2012	Xuan Lien NR, Thanh Hoa, Central	E, C				S			
<i>R. macrotis</i>	XL 47		♂	2012	Xuan Lien NR, Thanh Hoa, Central	E, C				S			
<i>R. macrotis</i>	XL 56	VN2446	♀	2012	Xuan Lien NR, Thanh Hoa, Central	E, C		KY652903		S	3		
<i>R. macrotis</i>	XL 57		♀	2012	Xuan Lien NR, Thanh Hoa, Central	E, C				S			
<i>R. macrotis</i>	XL 58		♀	2012	Xuan Lien NR, Thanh Hoa, Central	E, C				S			
<i>R. macrotis</i>	XL 61		♀	2012	Xuan Lien NR, Thanh Hoa, Central	C				S			
<i>R. macrotis</i>	VN11-0138	VN11-0138	♂	2011	Ba Be NP, Bac Kan, NE	E, C, G, B		KY652912		S	3		
<i>R. macrotis</i>	IEBR-M-469		♀	2002	Na Hang NR, Tuyen Quang, NE	C				S			
<i>R. macrotis</i>	IEBR-M-497		♂	2002	Na Hang NR, Tuyen Quang, NE	C				S			
<i>R. macrotis</i>	NTS 1669		♂	2002	Na Hang NR, Tuyen Quang, NE	E, C				S			
<i>R. macrotis</i>	NTS 1687			2002	Na Hang NR, Tuyen Quang, NE	E, C				S			
<i>R. macrotis</i>	B240514-17	VN3472	♀	2014	Na Hang NR, Tuyen Quang, NE	E		KY652902		S	3		
<i>R. macrotis</i>	NH16-58		♀	2016	Na Hang NR, Tuyen Quang, NE	E	66.0			S			
<i>R. macrotis</i>	NH16-62		♀	2016	Na Hang NR, Tuyen Quang, NE	E	66.1			S			

(Continues)

APPENDIX 1 (Continued)

Species	Field N°/Catalogue code	Tissue code	Sex	Year	Locality, Province, Region	Morphological examination	GenBank accession N°		
							FmaxE (KHz)	Cytb	COI
<i>R. macrotis</i>	POPD16.24		♂	2016	Phia Oac-Phia Den NR, Cao Bang, NE	E—External	67.3		S
<i>R. macrotis</i>	TD 47		♀	2005	Tam Dao NP, Vinh Phuc, NE	G—Glans penis B—Baculum			S
<i>R. macrotis</i>	B 200913.5		♂	2013	Tam Dao NP, Vinh Phuc, NE	E, C			S
<i>R. macrotis</i>	B 200913.8		♂	2013	Tam Dao NP, Vinh Phuc, NE	E, C			S
<i>R. macrotis</i>	VN15-07		♂	2015	Cuc Phuong NP, Ninh Binh, NW	E			S
<i>R. macrotis</i>	VN15-08		♂	2015	Cuc Phuong NP, Ninh Binh, NW	E			S
<i>R. macrotis</i>	VN15-09		♂	2015	Cuc Phuong NP, Ninh Binh, NW	E			S
<i>R. macrotis</i>	VN15-10		♂	2015	Cuc Phuong NP, Ninh Binh, NW	E			S
<i>R. macrotis</i>	VN3934B30	VN3934	♂	2014	Hoang Lien NP, Lao Cai, NW	E	69.8	KY652899	S
<i>R. macrotis</i>	VN3935B31	VN3935	♂	2014	Hoang Lien NP, Lao Cai, NW	E	68.9	KY652898	S
<i>R. macrotis</i>	B010713-3	KF2613	♀	2013	Khau Ca NR, Ha Giang, NW	E	68.3	KY652904	S
<i>R. macrotis</i>	XS15.28	VN4123	♀	2015	Xuan Son NP, Phu Tho, NW	E		KY652906	S
<i>R. macrotis</i>	VT Tu15-027	VTTu15-027	♂	2015	Phia Oac-Phia Den NR, Cao Bang, NE	E, C, B		KY652907	PO
<i>R. macrotis</i>	VT Tu15-028	VTTu15-028	♂	2015	Phia Oac-Phia Den NR, Cao Bang, NE	E, C		KY652908	PO
<i>R. macrotis</i>	POPD16.20		♂	2016	Phia Oac-Phia Den NR, Cao Bang, NE	E, C, G, B	43.2		PO
<i>R. marshalli</i>	XL 10		♂	2012	Xuan Lien NR, Thanh Hoa, Central	E, C			
<i>R. marshalli</i>	XL 11		♂	2012	Xuan Lien NR, Thanh Hoa, Central	E, C			
<i>R. marshalli</i>	XL 25		♀	2012	Xuan Lien NR, Thanh Hoa, Central	E, C			
<i>R. marshalli</i>	XS15.09		♀	2015	Xuan Son NP, Phu Tho, NW	E			
<i>R. marshalli</i>	XS15.20	VN4115	♂	2015	Xuan Son NP, Phu Tho, NW	E, C		KY652895	
<i>R. paradoxolophus</i>	IEBR-M-462		♀	2002	Na Hang NR, Tuyen Quang, NE	E, C			
<i>R. paradoxolophus</i>	IEBR-M-468		♀	2002	Na Hang NR, Tuyen Quang, NE	E, C			
<i>R. paradoxolophus</i>	IEBR-M-482		♀	2002	Na Hang NR, Tuyen Quang, NE	E, C			
<i>R. paradoxolophus</i>	IEBR-M-487		♂	2002	Na Hang NR, Tuyen Quang, NE	E, C			
<i>R. paradoxolophus</i>	NTS 1649		♂	2006	Na Hang NR, Tuyen Quang, NE	E, C			
<i>R. paradoxolophus</i>	NTS 1700		♂	2006	Na Hang NR, Tuyen Quang, NE	E, C			
<i>R. paradoxolophus</i>	IEBR-M-1905		♀	2008	Na Hang NR, Tuyen Quang, NE	E, C			
<i>R. paradoxolophus</i>	IEBR-M-1928		♂	2008	Na Hang NR, Tuyen Quang, NE	E, C			

(Continues)

APPENDIX 1 (Continued)

Species	Field N°/Catalogue code	Tissue code	Sex	Year, Locality, Province, Region	Morphological examination	GenBank accession N°			
						FmaxE (KHz)	Cytb	COI	Morp-form Clade
<i>R. paradoxolophus</i>	NH16-65		♀	2016, Na Hang NR, Tuyen Quang, NE	E	28.0			
<i>R. paradoxolophus</i>	NH16-66		♀	2016, Na Hang NR, Tuyen Quang, NE	E	28.6			
<i>R. paradoxolophus</i>	VN3477B47	VN3477	♀	2014, Na Hang NR, Tuyen Quang, NE	E			KY652897	
<i>R. paradoxolophus</i>	VTTu15-006		♂	2015, Trung Khanh, Cao Bang, NE	E, C				
<i>R. paradoxolophus</i>	KF2600	KF2600	♂	2013, Khau Ca NR, Ha Giang, NE	E			KY652896	

NR, nature reserve; NP, national park; NE, northeastern Vietnam; NW, northwestern Vietnam; M, R. cf. *macrotis*; S, R. cf. *siamensis*; PO, R. cf. *macrotis* Phia Oac