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A new species of *Hipposideros* (Chiroptera: Hipposideridae) from Vietnam

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A new species of *Hipposideros* is described from Vietnam. Morphologically, it is similar to taxa in the *Hipposideros armiger* complex but is substantially smaller. The new species, which has been found living sympatrically with *H. armiger* in Cat Ba National Park, is distinguished from it by size, acoustic characters, and differences in the mitochondrial DNA. Currently, the new taxon is known from Cat Ba Island in Ha Long Bay in northern Vietnam and from Chu Mom Ray National Park, which is situated on the mainland some 1,000 km to the south. It was collected in disturbed and primary forests.

Key words: bats, echolocation, hipposiderid, Mammalia, phylogenetics, taxonomy

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To date, the genus *Hipposideros* consists of 70 species worldwide (Bates et al. 2007; Guillén-Servent and Francis 2006; Helgen 2007; Simmons 2005). Within the Indomalayan region, species of *Hipposideros* are classified into 5 groups: *bicolor, pratti, armiger, speoris,* and *diadema* (Borissenko and Kruskop 2003; Corbet and Hill 1992; Hendrichsen et al. 2001; Simmons 2005; Thong 2011). The *armiger*-group is clearly distinguished from the remaining groups by the triangular shape of the ears, each with a bluntly pointed tip, and by the structure of the nose leaf, notably the ''fleshy outgrowths behind posterior leaf'' (Corbet and Hill 1992:106). According to Corbet and Hill (1992), the *armiger*-group comprises 2 species, *H. armiger* (Hodgson, 1835) and *H. turpis* (Bangs, 1901). Both forms can be well distinguished by their morphological and molecular characteristics (Thong 2011; Thong et al., in press). However, the taxonomic status of the subspecies within *H. armiger* sensu lato (s.l.) including *H. a. debilis* (Andersen, 1906) remains uncertain because the assignment of several taxa, which were described as subspecies or even species, is still debated. Currently 4 such taxa can be regarded as members of *H. armiger* s.l.: *armiger* sensu stricto (s.s.), *terasensis* Kishida, 1924, *fujianensis* Zhen, 1987, and *tranninhensis* Bourret, 1942. Yoshiyuki (1991) reclassified *terasensis* as a species distinct from *H. armiger* s.s. Subsequently, some authors followed this reclassification (e.g., Cheng and Lee 2002; Hiryu et al. 2006), whereas others (Corbet and Hill 1992; Ho and Lee 2003; Simmons 2005) considered *terasensis*, *fujianensis*, and *tranninhensis* as subspecies of *armiger* s.s. Similarly, Xu et al. (2010:9) suggested that all 3 Chinese subspecies of *H. armiger* s.l. (*armiger* s.s., *fujianensis*, and *terasensis*) are ''likely to be just *H. a. armiger.*'' Noticeably, the *turpis* species complex (Corbet and Hill 1992; Simmons 2005) is now recognized to comprise 3 distinct species: *H. turpis*, *H. pendleburyi*, and *H. alongensis* (Thong et al., in press).

To elucidate the taxonomic status of these species, we conducted a series of bat surveys in different areas of Vietnam between 2006 and 2009, with particular emphasis on catching hipposiderid bats. A total of 308 hipposiderid bats were captured during our surveys. Of these, we found 11 individuals belonging to the *armiger*-group that differed from all known taxa of *Hipposideros* based on morphological, molecular, and acoustic data; as such they represent a new species, which is described herein.

Materials and Methods

Bat capture.—Bats were captured and handled in the field following guidelines approved by the American Society of Mammalogists (Sikes et al. 2011). Four-bank harp traps (Francis 1989) and mist nets of various sizes (height 2.6 m, length 3–12 m, and mesh size 16 × 16 mm) were employed to capture bats. Each captured bat was removed carefully from the trap or net and placed individually in a cotton bag.

Morphometric measurements.—The following external and craniodental measurements were taken using a digital caliper to the nearest 0.1 mm. FA, forearm length—from the extremity of the elbow to the extremity of the carpus with the wings folded; EH, ear height—length of ear conch; EW, ear width—the greatest width of ear conch; ANW, anterior nose-leaf width—the greatest width of the anterior leaf; TIB, tibia length—from the knee joint to the ankle; HF, hind-foot length—from the extremity of the heel behind the os calcis to the extremity of the longest digit, excluding the hairs or claws; SL, total length of skull—from occiput to the most anterior part of the canine; CCL, condylocanine length—from the exoccipital condyle to the most anterior part of the canine; RW, rostrum width—measured in front of the anterior ramus of the anteorbital bar; IOW, interorbital width—the least width of the interorbital constriction; ZW, zygomatic width—the greatest width of the skull across the zygomatic arches; MW, mastoid width—the greatest distance across the mastoid region; C1–C1, width across the upper canines—greatest width, taken across the outer borders of upper canines; M3–M3, width across the upper molars—greatest width, taken across the outer crowns of the last upper molars; C1–M3, maxillary toothrow length—from the front of upper canine to the back of the crown of the 3rd molar; C1–P4, upper canine–premolar length—from the front of the upper canine to the back of the crown of the posterior premolar; ml, mandible length—from the anterior rim of the alveolus of the 1st lower incisor to the most posterior part of the condyle; c1–m3, mandibular toothrow length—from the front of the lower canine to the back of the crown of the 3rd lower molar; c1–p4, lower canine–premolar length—from the front of the lower canine to the back of the crown of the posterior premolar. The above measurements are illustrated in Bates and Harrison (1997) and Csorba et al. (2003). Reproductive status and age were assessed following Racey (2009) and Brunet-Rossinni and Wilkinson (2009), respectively. Body mass (BM) was taken in the field within 1 h after capture using a 50-g LightLine spring balance (PESOLA AG, Baar, Switzerland). To reduce the influence of seasonal variations in body mass, juveniles and pregnant females were excluded from analyses.

A list of museum specimens used as comparative material is given in Appendix I.

Acronyms for institutions mentioned in the text are as follows: IEBR-T.—Vu Dinh Thong collection, retained in the Institute of Ecology and Biological Resources (IEBR), Hanoi, Vietnam; BM(NH)—Natural History Museum, London, formerly British Museum (Natural History), United Kingdom; HNHM—Hungarian Natural History Museum, Budapest, Hungary; HZM—Harrison Institute, Sevenoaks, formerly Harrison Zoological Museum, United Kingdom; MNHN-ZM—Muséum National d'Histoire Naturelle, Paris, France; PSUZC-MM—Zoological Collection of Princess Maha Chakri Sirindhorn Natural History Museum, Prince of Songkla University (PSU), Hat Yai, Thailand; 4 material codes of *Hipposideros larvatus* (Hlar01, Hlar20, Hlar30, and Hlar37) correspond to tissue samples of released animals.

Recording and analysis of echolocation signals.—Echolocation calls were obtained from recordings in 3 situations inside a flight tent (4 m [length] × 4 m [width] × 2 m [height]): handheld (H), resting (R) on the wall, and flying (F) using a PCTape system at a sampling rate of 480 kHz. Batman software, which displays color sonograms of the detected echolocation signals in real time, was used to obtain high-quality sound sequences. Additionally, continuous recordings were carried out in front of caves and under forest canopies to obtain echolocation calls when bats were leaving their roosts and foraging in natural habitat, respectively. All echolocation signals from manual recordings inside the flight tent and a total of 120 min of sound sequences from these continuous recordings were analyzed using Selena software to measure the constant frequency of the 2nd harmonic (CF_2) of each call. We displayed a 5-s-long sequence from each individual as color spectrograms with a frequency range between 50 and 90 kHz (fast Fourier transform 8,192) and used the cursor to determine the frequency of the constant-frequency component with an accuracy of 58 Hz. The PCTape system and Batman and Selena softwares are custom-made by the Department of Animal Physiology, Faculty of Sciences, University of Tübingen (Tübingen, Germany).

Tissue sampling and genetic analysis.—Tissues for genetic analyses were taken from a subset of individuals using wing punches from released individuals or samples from specimens retained as vouchers in different collections. DNA was isolated using a modified salt–chloroform extraction protocol (Miller et al. 1988), which included an additional chloroform–isoamyl alcohol (24:1) step after the addition of the saturated NaCl solution. A 1,638-base pair (bp) fragment including the entire cytochrome-*b* gene and partial D-loop was amplified using the primers mtDNA-R3-F (5′-TGGCATGAAAAAT-CACCGTTGT-3′) and mtDNA-F2-R (5′-ATGGCCCTGAA-GAAAGAACCAGATG-3′—Puechmaille et al. 2011). Reactions were carried out in 25-μl simplex reactions containing 2 μl of DNA extract, 1X PCR buffer minus Mg (Invitrogen, Dublin, Ireland), 1.5 mM of $MgCl_2$, 0.4 μM of each primer, 0.2 mM of deoxynucleoside triphosphates, and 1 U of Platinum *Taq* DNA Polymerase High Fidelity (Invitrogen). Amplifications were carried out in a DNA Engine DYAD thermocycler (MJ Research, Waltham, Massachusetts) with the following polymerase chain reaction program: initial step 15 min at 95°C, then 10 cycles of 30 s at 95°C, 30 s at 60°C (with a reduction of 2°C every 2 cycles), 1 min 45 s at 72°C, followed by 30 cycles of 30 s at 95°C, 30 s at 50°C, and 1 min 45 s at 72°C, and a final step of 10 min at 72°C. Polymerase chain reaction products were purified and sequenced in both

Table 1.—External measurements (in mm) and echolocation frequency (in kHz) of *Hipposideros griffini*, new species, and *H. armiger*. Values are given as mean ± *SD*, minimum–maximum, sample size in parentheses. Abbreviations are defined in the "Materials and Methods."

Species	Specimen type, *n*	Sex	Morphological measurements						CF_2	
			FA	EH	EW	ANW	TIB	HF	H	R	F
H. griffini, new species	3	♀♀	85.2 ± 2.1	28.2 ± 0.8					77.5 ± 0.3	77.4 ± 0.5	77.4 ± 0.5
			83.3–87.5	27.5–29.0	24.5, 25.0 (2)	8.5, 9.0 (2)	35.2 (1)	15.7 (1)	77.2–77.7	76.8–77.7	76.8–77.8
	7	♂♂	87.1 ± 2.3	29.1 ± 0.8	24.8 ± 1.0	7.9 ± 0.7	38.0 ± 1.7	15.0 ± 0.8	77.2 ± 1.2	77.4 ± 0.5	77.1 ± 0.6
			83.5–90.0	28.0–30.0	23.5–26.5	7.0–8.5 (5)	36.4–40.1 (4)	14.1–15.8 (4)	75.5–79.2	76.4–78.0	76.2–77.8
H. a. tranninhensis	Holotype	♂	88.9	30.2	23.0		41.1				
H. a. armiger	27	♀♀	91.2 ± 2.7	30.7 ± 1.6			38.5 ± 1.9		66.5 ± 1.3	66.8 ± 1.4	67.1 ± 1.0
			85.6–98.9	28.1–33.0 (22)			36.6–43.4 (13)		64.7–68.8 (10)	64.9–68.8 (9)	65.9–68.6 (7)
	24	♂♂	93.4 ± 3.1	30.0 ± 1.1			40.2 ± 1.8		66.4 ± 1.2	66.7 ± 1.2	66.9 ± 1.1
			87.0–102.5	28.2–31.9 (15)			38.0–44.1 (14)		65.0–67.8 (6)	65.1–68.3 (6)	65.3–67.9 (5)
H. a. terasensis	3	♀♀	94.1 ± 2.2	29.8 ± 1.6			40.7 ± 0.6				
			92.7–96.7	28.6–31.6			39.9–41.0				
	5	♂♂	95.0 ± 4.1	30.1 ± 1.7			41.1 ± 1.5				
			88.1–98.8	28.2–32.5			39.5–42.9				

directions by Macrogen (Seoul, South Korea) using the polymerase chain reaction primers mentioned above and 3 additional internal primers, namely, mtDNA-F3-R (5′-AGGATGGCGTATGCAAATAGGAA-3′—Puechmaille et al. 2011), col-F3 (5′-CCAGACTTAYTAGGWGACCCAGA-3′—S. J. Puechmaille, pers. comm.), and mtDNA-F3b-R (5′-CCAAGTTTRTTTGGGATTGA-3′—S. J. Puechmaille, pers. comm.). Complementary sequences were assembled and edited for accuracy using CodonCode Aligner 3.7.1 (CodonCode Corporation, Dedham, Massachusetts). All sequences were submitted to GenBank (accession numbers JN247016–JN247046). Phylogenetic reconstructions were completed using the Bayesian inference in BEAST version 1.6.1 (Drummond and Rambaut 2007). The Hasegawa, Kishino, and Yano 1985 + gamma-distributed rates among sites + proportion of invariant sites (HKY+Γ+I) substitution model was used as determined by MODELTEST version 3.7 (Posada and Crandall 1998). No outgroup was specified and the Yule process was used as a tree prior along with a strict molecular clock model, which was preferred over a relaxed molecular clock model as advised by Drummond et al. (2007) when the standard deviation of the uncorrelated lognormal relaxed clock is smaller than one as observed with our data set. The unweighted pair-group method using arithmetic averages was used to construct the starting tree. The program was run for 20,000,000 generations and sampled every 500. The first 2,000,000 generations were discarded as burn-in. Two replicate analyses were performed to ensure convergence and the results were then pooled. Effective sample sizes for the estimated parameters and posterior probability as calculated with the program Tracer version 1.4 (Drummond and Rambaut 2007) were higher than 250.

Maximum-likelihood analyses were performed with PAUP version 4.0b10 (Swofford 2003) using the HKY+Γ+I substitution model following parameters settings estimated by MODELTEST (Posada and Crandall 1998): TRatio = 8.9170; base frequencies = (0.3131, 0.2977, 0.1199, 0.2693); proportion of invariant sites = 0.5776; and shape parameter of gamma distribution = 0.9447. Starting trees were obtained via neighbor-joining and analyses carried out using tree-bisection-reconnection–based heuristic searches. Sets of identical sequences (haplotypes) were constrained to be monophyletic. Bootstrap analyses included 100 replicates.

Estimates of sequence divergence over mitochondrial DNA (cytochrome-*b* and D-loop) sequence pairs between and within taxa were estimated using the Kimura 2-parameter method in MEGA4 (Tamura et al. 2007). Positions containing missing data were eliminated in pairwise sequence comparisons only.

Results

Hipposideros griffini *Thong et al., new species*

Holotype.—IEBR-T.200809.12, adult male, in alcohol, skull extracted, collected by Vu Dinh Thong on 20 August 2009. Measurements (in mm) are as follows: FA = 87.0; EH = 29.5; EW = 23.5; ANW = 8.0; TIB = 36.7; HF = 14.4; SL = 29.6;

Table 2.—Craniodental measurements (in mm) of *Hipposideros griffini*, new species, and *H. armiger*. Values are given as mean ± *SD*, minimum–maximum, sample size in parentheses. Abbreviations are defined in the ''Materials and Methods.''

Species	Specimen type, *n*	Sex	SL	CCL	RW	IOW	ZW	MW
H. griffini, new species	1	♀	29.2	25.5	8.6	3.7	16.3	13.6
	5	♂♂	29.6 ± 0.5	26.0 ± 0.4	8.9 ± 0.2	4.1 ± 0.1	16.5 ± 0.2	14.3 ± 0.2
			28.9–30.0	25.5–26.5	8.6–9.2	3.9–4.3	16.2–16.8	14.0–14.6
H. a. tranninhensis	Holotype	♂	32.0	28.0	9.8	4.0	18.2	15.0
	Paratype	♀			10.1	4.2	18.1	
H. a. armiger	14	♀♀	31.8 ± 0.4	28.0 ± 0.3	9.7 ± 0.1	4.3 ± 0.2	17.6 ± 0.2	15.0 ± 0.2
			30.8–32.3 (13)	27.4–28.5 (13)	9.4–9.9	3.9–4.6	17.3–18.1	14.4–15.4
	24	♂♂	32.3 ± 0.6	28.4 ± 0.7	9.8 ± 0.2	4.3 ± 0.2	18.0 ± 0.6	15.3 ± 0.3
			30.9–33.4 (22)	27.1–29.8 (16)	9.2–10.1 (19)	4.0–4.8 (19)	16.9–19.2 (19)	14.7–16.1 (18)
H. a. debilis	8	♀♀	31.2 ± 0.5	27.4 ± 0.5	9.5 ± 0.3	4.1 ± 0.2	17.5 ± 0.5	14.5 ± 0.2
			30.5–31.7 (6)	26.8–28.0 (6)	9.1–9.9	3.8–4.4 (7)	17.0–18.2 (6)	14.0–14.7 (6)
	4	♂♂			9.6 ± 0.2	4.0 ± 0.1		
			31.9, 33.0 (2)	28.0, 28.2 (2)	9.3–9.8	3.9–4.2	17.5, 19.0 (2)	14.4, 15.1 (2)
H. a. terasensis	5	♀♀	31.9 ± 0.6	28.1 ± 0.5	9.7 ± 0.3	4.4 ± 0.2	17.7 ± 0.3	15.0 ± 0.4
			31.0–32.5	27.3–28.7	9.3–10.0	4.1–4.7	17.4–18.0	14.6–15.5
	3	♂♂	32.4 ± 0.6		9.8 ± 0.2	4.3 ± 0.2	18.1 ± 0.5	15.6 ± 0.1
			31.8–33.0	28.0, 28.7 (2)	9.7–10.0	4.2–4.5	17.6–18.5	15.5–15.7

CCL = 25.8; RW = 9.1; IOW = 4.2; ZW = 16.5; MW = 14.4; C1–C1 = 7.7; M3–M3 = 11.7; C1–M3 = 11.4; C1–P4 = 5.2; ml = 20.3; c1–m3 = 12.6; c1–p4 = 4.7; BM = 44.0 g. Echolocation: H = 77.4 kHz; R = 77.1 kHz; F = 77.1 kHz.

Type locality.—Cat Ba National Park, Cat Ba Island, Ha Long Bay, Vietnam, 20°48′N, 107°01′E, 248 m above sea level (m a.s.l.).

Paratypes.—IEBR-T.200809.1, adult male; IEBR-T.200809.9, adult female; HNHM 2010.42.7 (field no. T.200809.14), adult male; bodies in alcohol; skulls extracted. These 3 paratypes also were collected from the type locality on 20 August 2009.

Etymology.—*Hipposideros griffini* was initially recognized as distinct by its echolocation frequency. It is named after the late Professor Donald Redfield Griffin (1915–2003) of Rockefeller University (New York), in recognition of his initiation and essential contributions to bat echolocation research. The proposed English and Vietnamese names are Griffin's leaf-nosed bat and Dơi nếp mũi Grip-phin, respectively.

Referred material.—IEBR-T.240608.2, 1st-year male, collected on 24 June 2008; IEBR-T.270608.6, adult male, collected on 27 June 2008; plus 1 released 1st-year female and 1 released adult female, captured on 27 June 2008, from

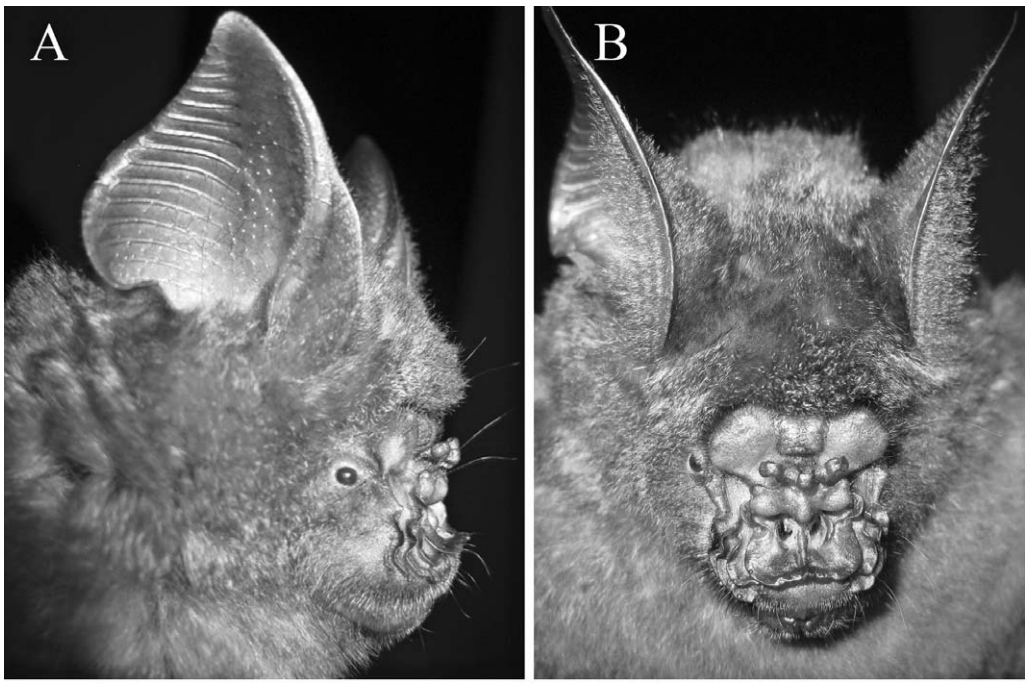

Fig. 1.—A) Lateral and B) frontal views of ear and nose leaves of *Hipposideros griffini*, new species (IEBR-T.200809.12, holotype). Not to scale.

Table 2.—Extended.

C1–C1	M3–M3	C1–M3	C1–P4	ml	c1–m3	c1–p4
7.3	11.1	11.3	5.2	19.9	12.4	4.7
7.7 ± 0.2	11.4 ± 0.2	11.4 ± 0.1	5.3 ± 0.2	20.5 ± 0.5	12.6 ± 0.1	4.7 ± 0.1
7.4–7.9	11.1–11.7	11.3–11.5	5.1–5.5	19.9–21.2	12.5–12.7	4.6–4.9
8.2	12.1 12.1	12.2	6.4	22.6	13.8	5.0
8.8 ± 0.2	12.5 ± 0.2	12.3 ± 0.2	5.6 ± 0.1	22.0 ± 0.3	13.5 ± 0.2	5.0 ± 0.1
8.4–9.2	12.0–12.8	11.9–12.6	5.4–5.9	21.1–22.4	13.1–13.8	4.8–5.2
8.9 ± 0.3	12.7 ± 0.4	12.5 ± 0.3	5.7 ± 0.2	22.4 ± 0.5	13.8 ± 0.3	5.0 ± 0.2
8.1–9.5 (18)	11.6–13.6 (19)	11.9–13.1	5.3–6.1 (19)	21.3–23.1 (19)	13.0–14.2 (19)	4.5–5.3 (19)
8.3 ± 0.4	12.4 ± 0.4	12.2 ± 0.3	5.5 ± 0.1	21.9 ± 0.5	13.3 ± 0.4	4.9 ± 0.2
7.6–8.9 (6)	12.0–12.9	11.7–12.7	5.3–5.7 (7)	21.3–22.7	12.8–14.0	4.7–5.2
8.5 ± 0.4	12.5 ± 0.5	12.4 ± 0.3	5.7 ± 0.2	22.7 ± 0.5	13.6 ± 0.4	5.2 ± 0.2
8.1–9.1	11.9–13.1	12.1–12.8	5.6–6.0	22.4–23.3 (3)	13.4–14.2	4.9–5.4
8.5 ± 0.4	12.6 ± 0.4	12.6 ± 0.3	5.8 ± 0.2	22.1 ± 0.5	13.7 ± 0.4	5.0 ± 0.2
8.1–8.9	12.1–13.0	12.1–12.9	5.6–6.0	21.4–22.6	13.3–14.1	4.8–5.3
8.9 ± 0.1	12.9 ± 0.2	12.6 ± 0	5.8 ± 0.1	22.4 ± 0.3	13.7 ± 0.1	5.1 ± 0.1
8.9–9.0	12.7–13.1	12.6–12.7	5.7–5.9	22.0–22.6	13.6–13.8	5.0–5.2

Chu Mom Ray National Park, Kon Tum Province, Vietnam, 14°25′N, 107°44′E, 656 m a.s.l.; plus 2 released adult males and 1 released 1st-year male, captured on 20 August 2009 from the type locality.

Diagnosis.—Forearm length 83.3–90.0 mm (Table 1). The anterior nose leaf has 4 supplementary leaflets of which the 2nd is the widest and longest, whereas the 4th (outermost) is the narrowest and shortest (Fig. 1). The 3rd leaflet connects posteriorly to a developed sexual outgrowth. The skull is robust with a greatest length of 28.9–30.0 mm (Table 2). Generally, the preorbital ridge is gracile and nearly straight forming a very large infraorbital foramen. The posterior emargination of the palate is almost rounded (Fig. 2). The 1st upper premolar is minute and situated outside the toothrow. The species uses echolocation calls with a CF_2 value of 75.5–79.2 kHz (Table 1).

Description.—Externally, this is a very large *Hipposideros* with forearm length of 83.3–90.0 mm ($n = 11$). The general pelage color varies from brown to gray. The dorsal fur is darker than the ventral fur and in all hairs, the upper one-third is darker than the remaining part. The anterior leaf is broad anteriorly. Posteriorly, it is also broad and passes behind the base of the intermediate leaf. It is at its narrowest just in front of the base of the intermediate leaf (Fig. 1). Its greatest width is 7.0–8.5 mm (Table 1). There is a narrow median notch on its anterior edge. There are 4 pairs of supplementary lateral leaflets. Of these, the 2nd appears as the most developed, whereas the 4th is short and ill-defined; the 3rd is attached posteriorly to a fleshy outgrowth. The anterior nose leaf and 4 supplementary leaflets are fleshy and naked. The outer parts of the anterior nose leaf and each of the lateral leaflets are darker than their inner parts. The internarial septum is thin and slightly swollen medially. The intermediate leaf, which has a swollen median septum, is almost equal in width to the narrowest part of the anterior leaf and is substantially wider than the posterior leaf. The upper border of the posterior leaf is almost cuspidate. Behind the posterior leaf of each adult male, there is a well-developed fleshy outgrowth and a sexual sac, which is considerably enlarged during the breeding season (Fig. 1). The pinna of each ear is 23.5–26.5 mm and 27.5–30.0 mm in width and height, respectively (Table 1). It has a bluntly pointed tip and a slightly convex anterior margin. On its posterior margin, the upper one-third is concave, whereas the remainder is convex (Fig. 1).

The total length and condylocanine length of the skull are 28.9–30.0 mm and 25.5–26.5 mm, respectively (Table 2). The zygomatic arch is generally gracile, slightly expanded posteriorly (Fig. 3). The anteorbital foramen is quite large and has a nearly straight, gracile bone above. The anterior median swellings of the rostrum are more inflated than the posterior and lateral ones. The sagittal crest is greatly developed. The palate is emarginated anteriorly to a point equal to the anterior margin of the 1st upper molar, and posteriorly to a point corresponding roughly to the middle of the 3rd upper molar. The posterior incision of the palate is usually tapering (Fig. 2). Although both the cochlea and tympanic bulla are well developed, the former is more inflated. The mandible is very robust, and has a greatly developed coronoid process, which slightly exceeds the respective lower canine in height.

In the dentition, the upper and lower incisors are considerably developed, and bifid and trifid, respectively. Upper toothrow length is 11.3–11.5 (Table 2). The upper canine is very robust and has a deep vertical groove on its inner side and a sharp posterior edge. The 1st upper premolar is minute and nearly circular in crown shape, and situated outside the toothrow. All the cheek teeth are well developed and the W-shape cusp patterns on the surface of the 1st and 2nd upper molars are clearly defined. The 1st and 2nd upper molars are subequal in size, whereas the 3rd upper molar is small, about 40% of the 2nd upper molar in size. The lower canine also is well developed and has vertical grooves on its inner and posterior surfaces. The 1st lower premolar is

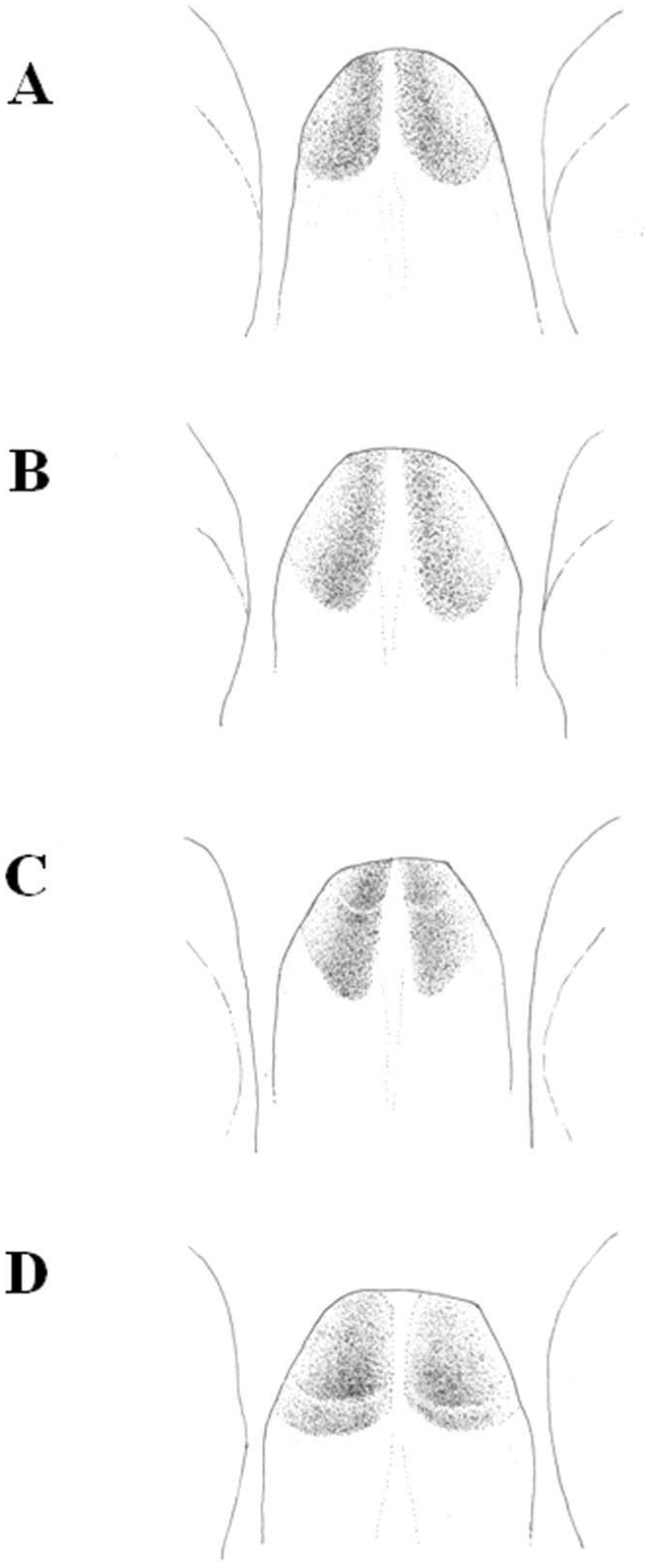

Fig. 2.—Posterior palatal emargination of A) *Hipposideros griffini*, new species (Cat Ba Island, IEBR-T.200809.12, holotype); B) *H. armiger* (Cat Ba Island, HNHM 98.90.32); C) *H. armiger armiger* (Nepal, HNHM 98.9.1, topotype); and D) *H. armiger tranninhensis* (Vietnam, MNHN CG 2007.120, paratype). Not to scale.

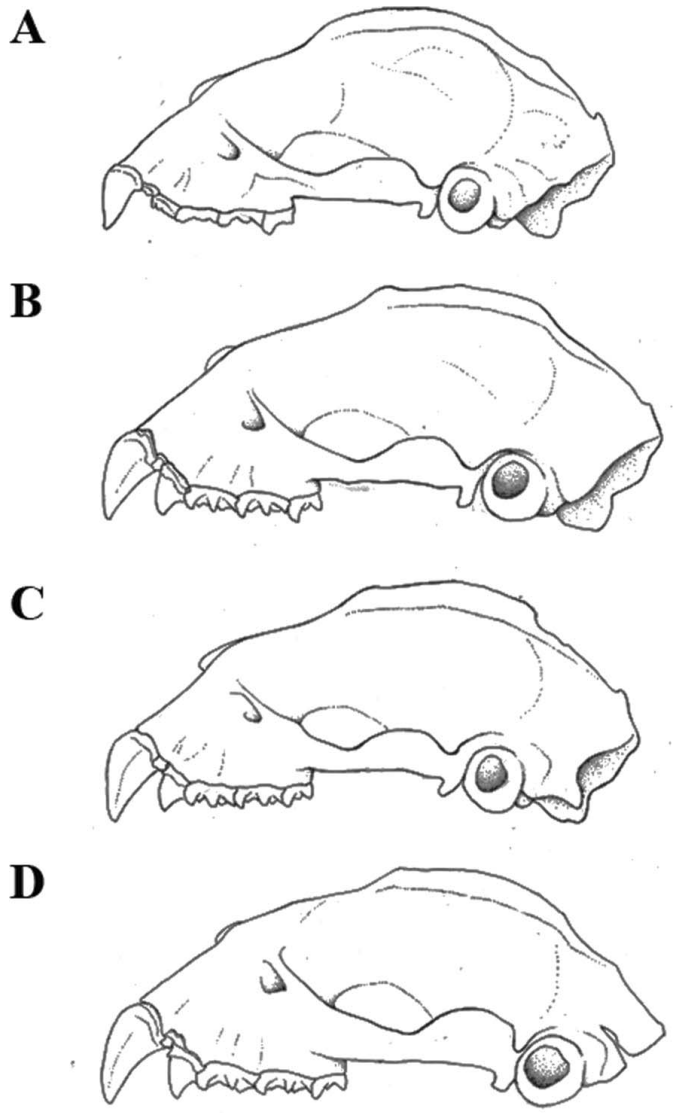

Fig. 3.—Lateral view of skulls of A) *Hipposideros griffini*, new species (Cat Ba Island, IEBR-T.200809.12, holotype); B) *H. armiger* (Cat Ba Island, HNHM 98.90.32); C) *H. armiger armiger* (Nepal, HNHM 98.9.1, topotype); and D) *H. armiger tranninhensis* (Vietnam, MNHN 1948-361, holotype). Scale = 10 mm.

approximately 50% of the 2nd lower premolar in both height and crown area. The 2nd lower premolar is taller than the 1st lower molar but considerably smaller in crown area. The 1st and 2nd lower molars are subequal in both height and crown area, whereas the 3rd is reduced, its crown area being about two-thirds that of the 2nd molar.

The baculum is small and gracile with a total length of approximately 1.9 mm. There is a well-indicated depression in the base. The shaft clearly bends ventrally, has a well-defined vertical median groove on its ventral surface, and is expanded toward the base. The tip of the baculum is deeply bifid, forming a fork (Fig. 4). Two branches of the fork are clearly convex and tapering upward.

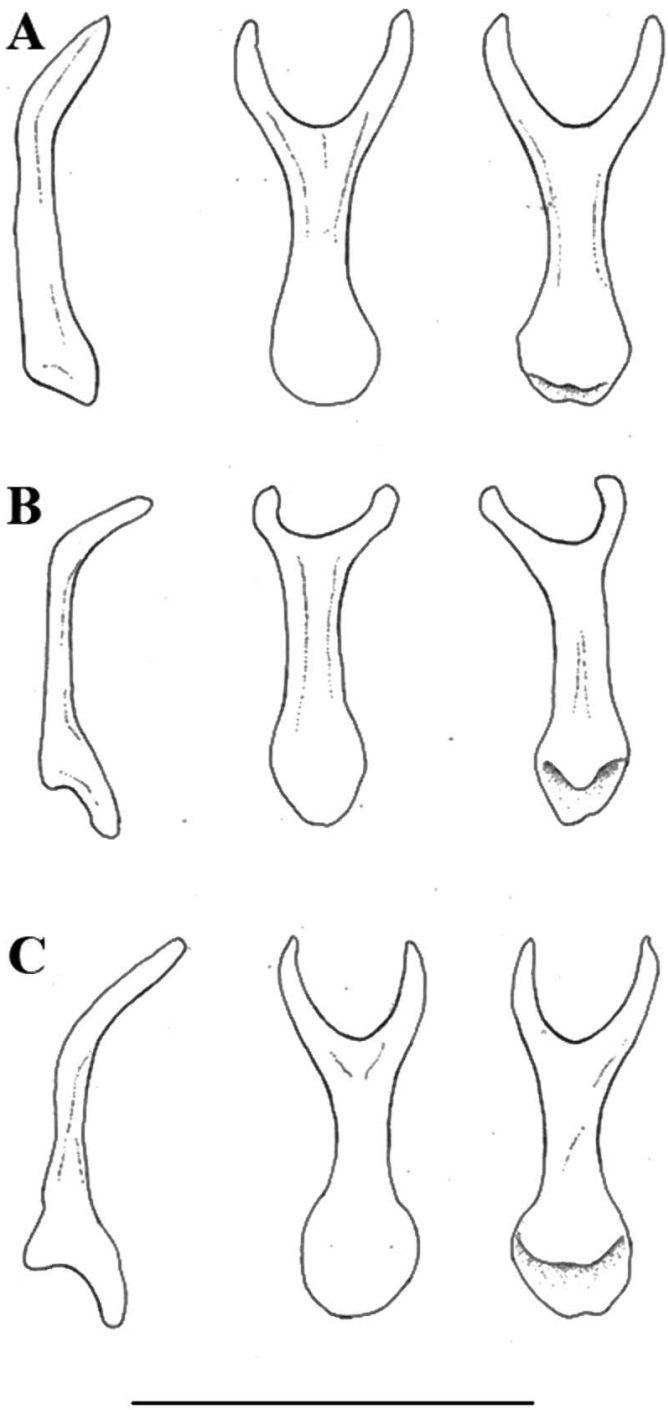

Fig. 4.—Lateral (left), ventral (central), and dorsal (right) views of baculum of A) *Hipposideros griffini*, new species (IEBR-T.200809.12, holotype); B) *H. armiger armiger* (Cat Ba, IEBR-T.090909.1); and C) *H. a. armiger* (Nepal, HNHM 98.5.27, topotype). Scale = 2 mm.

Echolocation.—Hipposideros griffini uses the typical multi-harmonic calls of hipposiderid bats with the maximum energy in the 2nd harmonic. Each signal comprises 3 components: a short initial frequency-modulated component, followed by a long component of constant frequency and a short terminal frequency-modulated component. Frequency values for CF_2 in handheld, resting, and flying situations are 75.5–79.2 kHz (n = 11), 76.4–78.0 kHz (n = 11), and 76.2–77.8 kHz (n = 11), respectively. There is little difference in CF_2 between females (77.2–77.7 kHz, 76.8–77.7 kHz, 76.8–77.8 kHz; n = 3) and males (75.5–79.2 kHz, 76.4–78.0 kHz, 76.2–77.8 kHz; n = 7) in handheld, resting, and flying situations, respectively (Table 1). The CF_2 values obtained from continuous recordings also nest within the above variation of the flying situation. The above results, obtained from 2 far distant areas (Cat Ba National Park and Chu Mom Ray National Park) some 1,000 km apart, suggest that the CF_2 frequency of *H. griffini* shows limited geographic variation.

Genetic analyses.—The mitochondrial DNA tree recovered a well-defined monophyletic clade comprising *H. griffini* from Vietnam, *H. a. terasensis* from Taiwan, *H. pendleburyi* from Thailand, and *H. armiger* from Thailand, Myanmar, Lao People's Democratic Republic, and Vietnam (Fig. 5). Although Kimura 2-parameter sequence divergences between *H. a. terasensis* and *H. pendleburyi* compared to *H. armiger* were around 2%, *H. griffini* was 5.3–5.4% different from these 3 taxa (Table 3). These results indicate that *H. griffini* is genetically clearly distinct from closely related hipposiderids of the *armiger* group (Fig. 5).

Ecology and habitat.—Hipposideros griffini was found in both mountainous and karst areas with vegetation ranging from disturbed to primary forests. The holotype and all paratypes were collected from karst habitats, where forests are almost primary in structure, in Cat Ba National Park, an island in Ha Long Bay. The capture site of the type series belongs to the core zone of Cat Ba National Park containing dense vegetation with at least 3 distinct canopies. A large number of caves of various sizes occur within the park and its surroundings. Three individuals of the new species were captured at the Ba Gok section of Chu Mom Ray National Park, where the vegetation mostly consists of degraded forests and plantations. Other rhinolophoid bat species recorded at the same locality as *H. griffini* included *Aselliscus stoliczkanus*, *H. cineraceus*, *H. galeritus*, *H. larvatus*, *H.* cf. *pomona*, *H. alongensis*, *Rhinolophus affinis*, *R. pusillus*, and *R. macrotis*.

Reproductive biology.—A juvenile male was captured at Chu Mom Ray National Park in June. Almost all mature males of this species captured in August had well-developed fleshy outgrowths and sexual sacs, indicating that they were reproductively active.

Distribution.—Hipposideros griffini is known from 2 localities: Cat Ba National Park, Cat Hai District, and Chu Mom Ray National Park, Kon Tum Province. The former is situated on an offshore island in northern Vietnam and the latter on the mainland some 1,000 km to the south.

Discussion

Comparison of morphological data.—Externally, as a species of the *armiger*-group, *H. griffini* differs distinctly from members of the *bicolor*- and *speoris*-groups in both body size and nose-leaf structure and from species of the *diadema-*

TABLE 3.—Estimates of sequence divergence over cytochrome-*b* gene and D-loop (1,638 base pairs) sequence pairs between and within taxa of *Hipposideros*. The number of base substitutions per site from averaging over all sequence pairs between taxa (average: lower triangular matrix; *SD*: upper triangular matrix) and within each taxa (on the diagonal) is shown.

	H. griffini	*H. armiger*	*H. pendleburyi*	*H. a. terasensis*	*H. larvatus*	*H. lylei*	*H. turpis*
H. griffini	**0.20**	0.5	0.6	0.6	0.7	1.0	1.0
H. armiger	5.3	**2.00**	0.3	0.3	0.6	1.0	0.9
H. pendleburyi	5.4	2.0	**0.37**	0.4	0.7	1.0	1.0
H. a. terasensis	5.3	2.1	1.9	**0.04**	0.7	1.0	1.0
H. larvatus	9.0	8.1	8.0	8.0	**3.19**	0.8	0.9
H. lylei	12.8	12.8	12.6	13.2	12.0	**0.00**	0.8
H. turpis	13.3	12.9	12.6	12.9	13.3	8.1	**0.00**

and *pratti*-groups in nose-leaf structure (Bates and Harrison 1997; Borissenko and Kruskop 2003; Corbet and Hill 1992; Thong 2011). Within the *armiger*-group, *H. griffini* differs distinctly from *H. turpis*, *H. pendleburyi*, and *H. alongensis* in morphological, echolocation, and genetic aspects (Thong 2011; Thong et al., in press; Fig. 5).

Based on our detailed study of a series of *H. a. armiger*, *H. a. debilis*, *H. a. terasensis*, and *H. a. tranninhensis* (see Appendix I), these 4 subspecies are indistinguishable by their external and craniodental features; consequently we compare *H. griffini* with *H. armiger* at the species level. *H. griffini* is similar to *H. armiger* in external characteristics, but considerably smaller in body size (Table 1). Craniodentally, the skull and teeth of *H. griffini* are generally smaller than those of *H. armiger* (Table 2). The new species is further distinguished from *H. armiger* as follows. The zygomatic arch of *H. griffini* is usually narrow (Fig. 3), whereas that of *H. armiger* is thick, narrow anteriorly, and expanded posteriorly (Fig. 3). The posterior emargination of the palate of *H. griffini* is almost rounded, whereas that of *H. armiger* is squarish (Fig. 2). The preorbital ridge is generally straight in *H. griffini*, but is concave in *H. armiger*.

Comparison of echolocation data.—Echolocation frequencies of *H. griffini* (76.6–79.2 kHz) are distinctly higher than those of *H. a. armiger* (64.7–68.8 kHz), both in sympatric and allopatric populations, and of *H. a. terasensis* (65.9–71.4 kHz), which also reflects their differences in body size (Hiryu et al. 2006; Fig. 6; Table 1). These differences in CF_2 values further support our conclusion that *H. griffini* is a different species. In addition, there is little difference in CF_2 between *H. a. terasensis* and *H a. armiger*. There is no evidence of geographical variation in echolocation call frequencies of both *H. griffini* and *H. armiger* in Vietnam. In resting situations, the CF_2 values of *H. griffini* are 76.4–78.0 kHz ($n = 7$) and 76.8–77.7 kHz ($n = 4$) from Cat Ba National Park and Chu Mom Ray National Park, respectively. Within the study areas, *H. griffini* is distinguishable in echolocation frequencies from all known rhinolophoid species in Cat Ba National Park and Chu Mom Ray National Park (Thong 2011). Therefore, data from this study appear useful for acoustic identification of *H. griffini* in the field.

Phylogenetic relationships.—*Hipposideros griffini* forms a well-supported monophyletic clade basal to the *H. armiger* species complex. Comparison of the overlapping D-loop region (360 bp) from the present sequences (this study) with those from China (Xu et al. 2010) shows that none of the Chinese *H. armiger* so far sequenced belong to *H. griffini* (V. D. Thong, in

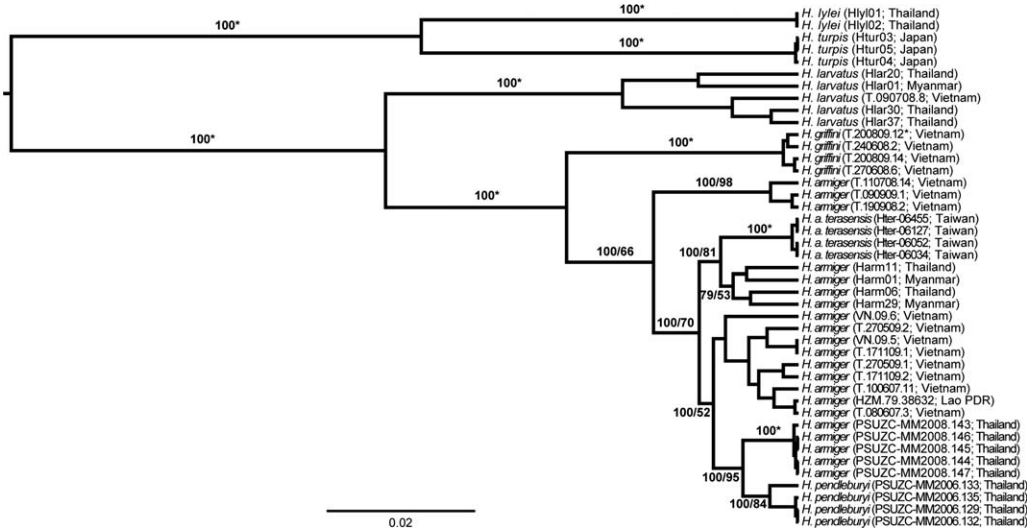

FIG. 5.—Bayesian tree (HKY+Γ+I substitution model) showing the phylogenetic relationship between individuals of different taxa based on 1,638 base pairs of the cytochrome-*b* gene and D-loop. Posterior probability (×100) and bootstrap support is shown above each branch of interest. Tip labels are composed of species names followed in brackets by specimen reference and country of origin. An asterisk (*) indicates the type specimen of *Hipposideros griffini*, new species.

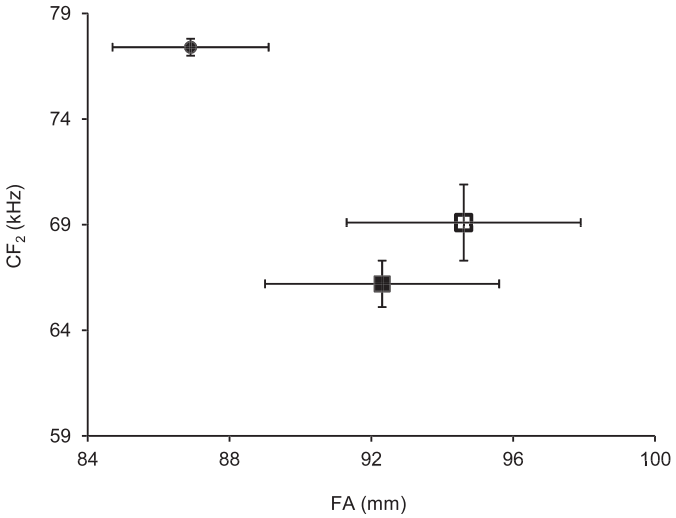

Fig. 6.—Relationship between echolocation frequencies and forearm lengths of *Hipposideros griffini*, new species (closed circle), *H. armiger armiger* (closed square) from Vietnam, and *H. a. terasensis* (open square—Hiryu et al. 2006; Table 1) from Taiwan.

litt.). In Vietnam, *H. griffini* is sympatric with *H. armiger* in Cat Ba National Park, which strengthens our conclusion that the former represents a new species as opposed to an isolated population of *H. armiger* with divergent mitochondrial DNA. Analyses of nuclear markers would be useful to confirm the absence of gene flow between *H. griffini* and *H. armiger*. Within-species divergence for *H. griffini* was low (0.2%, $n = 4$; Table 3) but without additional samples, it is difficult to ascertain whether this is a sample-size artifact or if the species has a low level of genetic diversity. Thong et al. (in press) reported on the paraphyly of *H. armiger* and suggested either a very recent divergence between *H. armiger* and *H. pendleburyi* or a recent introgression of *H. armiger* mitochondrial DNA into *H. pendleburyi*. Our results demonstrate that a similar situation might have happened between *H. armiger* and *H. a. terasensis*, the only difference being that presently, *H. a. terasensis* and *H. armiger* are not sympatric and, therefore, a very recent separation hypothesis would be favored. This recent separation could be directly linked to changes in sea level during the Pleistocene (Voris 2000). It is interesting to note that both *H. griffini* and *H. pendleburyi* are sympatric with *H. armiger* and both species echolocate at different frequencies compared to *H. armiger*, whereas *H. a. terasensis*, which is allopatric with *H. armiger*, echolocates with overlapping frequencies. These results suggest that echolocation frequency might play a role in speciation and further investigations into the phylogeography, population structure, and echolocation call variation in *H. griffini*, *H. armiger*, *H. a. terasensis*, and *H. pendleburyi* would be of great interest to better understand the role of sensory ecology in speciation.

Distribution.—The known distribution of *H. griffini* is clearly disjunct. Within Vietnam, there are a number of areas containing habitats similar to either Cat Ba National Park or Chu Mom Ray National Park. Further studies are required to determine if the species is present in other mainland areas of Cambodia, China, Lao People's Democratic Republic, Myanmar, Thailand, and Vietnam.

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APPENDIX I

To condense this appendix, only details of released individuals are given. Information on all voucher specimens is accessible from the corresponding museums.

Hipposideros armiger armiger (38 females, 43 males, and 12 unsexed).—**India**: HNHM.92.100.1 (♀), HNHM.92.100.2 (♀), HNHM.92.100.6 (♀), HNHM.92.100.7 (♀), HNHM.92.100.9 (♀), HNHM.92.147.1 (♀), HNHM.93.20.1 (♀), HNHM.93.20.4 (♀), HNHM.93.20.5 (♀), HNHM.93.20.6 (♀), HNHM.93.20.7 (♀), HNHM.93.21.1 (♀), HNHM.92.100.10 (♂), HNHM.92.100.3(♂), HNHM.92.100.4 (♂), HNHM.92.100.5 (♂), HNHM.92.100.8 (♂), HNHM.93.20.2 (♂), HNHM.93.20.3 (♂); **Lao People's Democratic Republic**: BM(NH).78.2336 (♀), HNHM.98.39.5 (♀), HNHM.98.39.12 (♂), HNHM.98.39.8 (♂), HZM.79.38632 (♂); **Myanmar**: BM(NH).50.422 (♀), HZM.17.35008 (♀), Harm01 (♀, released) and 2 (unsexed) released individuals, captured at Great Saddan Cave, Kayin State, 16°44′N, 97°43′E, 29 m a.s.l., BM(NH).50.419 (♂), BM(NH).50.420 (♂), BM(NH).50.421 (♂); **China**: BM(NH).8.1.30.1 (♂), BM(NH).8.1.30.2 (♂), BM(NH).8.7.25.1 (♂), BM(NH).8.7.25.2 (♂), BM(NH).11.9.8.8 (♂), BM(NH).11.9.8.9 (♂); **Hong Kong**: BM(NH).66.25 (♂); **Nepal**: HNHM.98.5.30 (♀), HNHM.98.5.31 (♀), HNHM.98.5.3 (♀), HNHM.98.5.32 (♀), HNHM.98.8.9 (♀), HNHM.98.9.1 (♀), HNHM.98.5.27 (♂), HNHM.98.8.10 (♂), HNHM.98.8.29 (♂), HNHM.98.8.8 (♂), HNHM.98.9.4 (♂); **Vietnam**: HNHM.93.53.1 (♀), HNHM.98.90.31 (♀), IEBR-T.10/04(01) (♀), IEBR-T.10/04(02) (♀), plus 3 (♀, released) from Thuong Lam Commune, Na Hang District, Tuyen Quang Province, 22°30′N, 105°19′E, 270 m above sea level (m a.s.l.), 1 (♀, released) from Dakrong Nature Reserve, Dakrong District, Quang Tri Province, 16°37′N, 106°53′E, 183 m a.s.l., 1 (♀, released) from Cai Lim Island, Bai Tu Long National Park, Quang Ninh Province, 21°07′N, 107°35′E, 6 m a.s.l.; 4 (♀, released) from Ba Be National Park, Bac Kan Province, 22°23′N, 105°36′E, 278 m a.s.l., HNHM.2007.27.6 (♂), HNHM.98.90.32 (♂), IEBT-T.080706.3 (♂), IEBT-T.190908.2 (♂), IEBT-T.100607.11 (♂), IEBT-T.110708.14 (♂), IEBR-T.02 (♂), IEBR-T.19/10 (15) (♂), IEBR-T.10/04 (03) (♂), IEBR-T.19/10 (13) (♂), IEBR-T.20.10.04 (19) (♂), IEBR-T.20.10.04 (18) (♂); **Thailand**: PSUZC-MM2008.143 (♀), PSUZC-MM2008.145 (♀), PSUZC-MM2008.146 (♀), BM(NH).2000.111.1 (♂), BM(NH).78.2337

(♂), PSUZC-MM2008.144 (♂), PSUZC-MM2008.147 (♂) from Kong Ka Lot Cave, Na Thon District, Satun Province, 7°7′N, 99°59′E, 86 m a.s.l., Harm11 (♂, released) and 4 (unsexed) released individuals, captured at Mae Usa Cave, Mae Kasa District, Tak Province, 16°53′N, 98°38′E, 341 m a.s.l., Harm06 (♂ released) and 4 (unsexed) released individuals, captured at Rathana Kiri Cave, Khao Kwang Thong District, Uthai Thani Province, 15°22′N, 99°40′E, 122 m a.s.l., 2 (unsexed) individuals released, captured at Tham Nam, Nang Kaeo District, Ratchaburi Province, 13°41′N, 99°45′E, 14 m a.s.l.

Hipposideros armiger debilis (8 females and 4 males).—**Malaysia**: BM(NH).56.157 (♀), BM(NH).56.158 (♀), BM(NH).56.159 (♀), BM(NH).34.7.18.21 (♀), BM(NH).34.7.18.22 (♀), BM(NH).60.5.4.3 (♀), BM(NH).? (♀), BM(NH).34.7.18.20 (♂), BM(NH).7.1.1.313 (♂), BM(NH).7.1.1.314 (♂), BM(NH).79.11.21.78 (♂), BM(NH).79.11.21.81 (♀).

Hipposideros armiger terasensis (5 females, 6 males, and 5 unsexed).—**Taiwan**: HNHM.2000.9.19 (♀), HNHM.2009.13.1 (♀), HNHM.2009.13.2 (♀), HNHM.2009.13.4 (♀), HZM.3.3523 (♀), HNHM.98.19.5 (♂), HNHM.2003.36.10 (♂), HNHM.2005.65.56 (♂), HNHM.2009.13.3 (♂), HNHM.2009.13.5 (♂), HZM.2.3522 (♂), Hter-06455(unsexed), Hter-06216(unsexed), Hter-06127(unsexed), Hter-06034(unsexed), Hter-06052(unsexed).

Hipposideros armiger tranninhensis (1 male and 1 unsexed).—**Vietnam**: MNHN-ZM 1948-361 (holotype) (♂); MNHN-ZM -? [CG no. 2007.120] (paratype) (unsexed).

Hipposideros lylei (2 females).—**Thailand**: 2 released females, captured at Mae Usa Cave, Mae Kasa District, Tak Province, 16°53′N, 98°38′E, 341 m a.s.l.

Hipposideros turpis (3 released individuals).—**Japan**: captured at Funauki, Iriomotejima Island, Okinawa (unsexed).

Hipposideros larvatus (2 females and 3 males).—**Myanmar**: Hlar01 (♂ released), captured at Kywe Cave, Kayin State, 16°49′N, 97°35′E, 59 m a.s.l.; **Thailand**: Hlar20 (♀ released), captured at Rathana Kiri Cave, Khao Kwang Thong District, Uthai Thani Province, 15°22′N, 99°40′E, 122 m a.s.l., Hlar37 (♀ released), captured at Tham Nam, Nang Kaeo District, Ratchaburi Province, 13°41′N, 99°45′E, 14 m a.s.l., Hlar30 (♂ released), captured at Tham Muang Cave, Kok Tum District, Lopburi Province, 14°48′N, 100°46′E, 77 m a.s.l.; **Vietnam**: IEBR-T.090708.8 (♂).