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A new species in the *Hipposideros bicolor* group (Chiroptera: Hipposideridae) from Peninsular Malaysia

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With 70 named species and multiple morphologically cryptic lineages, the genus *Hipposideros* is a diverse and taxonomically contentious group of insectivorous bats in the Old World tropics. Half of the named species and most of the cryptic diversity in *Hipposideros* are concentrated in the *bicolor* species group. Here we resolve the taxonomic status of *Hipposideros bicolor* (Temminck, 1834), the species group's namesake. Two morphologically cryptic but acoustically and genetically distinct lineages of *H. bicolor* co-occur in peninsular Malaysia and Thailand. Pending taxonomic revision, these lineages were named according to the average frequency of maximum energy of echolocation calls of populations in central peninsular Malaysia, *H. bicolor*-131 and *H. bicolor*-142. To determine the taxonomic status of the two lineages we measured cranial characters from all available type specimens in the *H. bicolor* species group, and collected morphometric, acoustic and mitochondrial DNA sequence data for *H. bicolor*-131, *H. bicolor*-142, and closely related lineages, from multiple localities on the Malay peninsula and Borneo. Consistent with prior studies, acoustic and genetic analyses strongly support species status for *H. bicolor*-131 and *H. bicolor*-142. We find subtle but significant differences in cranial characters, including a longer skull and longer upper and lower tooth rows in *H. bicolor*-131 relative to *H. bicolor*-142. Most importantly, inclusion of cranial measurements for type specimens in the *H. bicolor* species group indicates that *H. bicolor*-131 should retain the species name, while *H. bicolor*-142 is distinct from all previously named species. We therefore provide a complete description for this new species of bat from Southeast Asia, *Hipposideros kunzi* sp. nov.

Key words: cave roosting, Chiroptera, cryptic diversity, morphometrics, phonic type, Old World leaf-nosed bats, Sunda shelf, taxonomy

Introduction

The family Hipposideridae consists of a widespread and abundant group of insectivorous bats in the Old World tropics, with 84 named species inhabiting tropical and subtropical regions of Africa and the Middle East, through Asia and Australia (Simmons, 2005; Guillén-Servent and Francis, 2006; Thabah *et al*., 2006; Bates *et al*., 2007). The 70 species within the genus *Hipposideros* are grouped according to similarity in morphology, with nine species groups currently recognized (Simmons, 2005; but see Murray *et al*., 2012). The *bicolor* species group, comprising half of all named species in the genus *Hipposideros*, is by far the largest and most taxonomically problematic. Many of the species in the *bicolor* group share a similar appearance that does not necessarily indicate a close evolutionary relationship (e.g., Guillén-Servent and Francis, 2006; Thabah *et al*., 2006; Murray *et al*., 2012). Adding to the taxonomic confusion in this group, many of the original species descriptions are brief, lack diagnosable characters, and/or fail to declare a type specimen.

Hipposideros bicolor (Temminck, 1834) is thought to occur throughout Southeast Asia ranging from Laos and Vietnam through peninsular Malaysia to Borneo, the Philippines and Indonesia (Simmons, 2005). Within this distribution, two morphologically cryptic but genetically and acoustically distinct lineages of *Hipposideros bicolor* are co-distributed in peninsular Malaysia and Thailand (Kingston *et al*., 2001; Douangboubpha *et al*., 2010). The two lineages were identified based on

mitochondrial DNA sequence divergence and non-overlapping frequencies of maximum energy (of the CF component) of the echolocation call, centered at 142 and 131 kHz (Kingston *et al*., 2001). Kingston and colleagues proposed that the two phonic types, hereafter *H. bicolor*-142 and *H. bicolor*-131, represented distinct species (Kingston *et al*., 2001). While we and others confirmed that *H. bicolor* is polyphyletic (e.g., Khan *et al*., 2008; Murray *et al*., 2012; Esselstyn *et al*., 2012), the taxonomic history of the *bicolor* group is complex and the status of *H. bicolor*-142 and *H. bicolor*-131 has remained uncertain, pending examination of type material.

The original description of *Rhinolophus bicolor* Temminck, 1834 was based on a series of bats from Java, Ambon, and Timor (Temminck, 1834, 1835) housed in the Rijksmuseum van Natuurlijke Historie (now the Naturalis) in Leiden, Netherlands. The individuals from Ambon were smaller than those from Java, and were described as *Phyllorhina amboinensis* by Peters (1871). Tate (1941) found seven specimens in the Naturalis that Temminck may have used to describe *H. bicolor* and declared the largest specimen from Java as the lectotype. The remaining six specimens were listed as paralectotypes for *H. bicolor*: two specimens from Java and four individuals from Ambon that were also part of the *H. amboinensis* syntype series (C. Smeenk, personal communication). Tate (1941) failed to locate any individuals of *H. bicolor* from Timor that Temminck could have used in his description of the species.

In his revision of the genus *Hipposideros*, Hill (1963) concurred with Andersen (1918) that *H. bicolor* was a species of medium size whereas *H. gentilis* Andersen, 1918 and *H. pomona* Andersen, 1918 were larger forms. By designating the largest surviving specimen from Temminck's series as the lectotype of *H. bicolor*, Hill (1963) concluded that Tate (1941) had transferred the name *H. bicolor* to an individual of *H. gentilis.* Both Ellerman and Morrison-Scott (1951) and Hill (1963) considered *H. gentilis* to be conspecific with *H. pomona*, and therefore Hill (1963) placed *H. pomona* and *H. gentilis* (including *atrox*, *sinensis*, and *major*) as subspecies of *H. bicolor*. In addition, he placed *H. erigens* Lawrence, 1939, a species described from the Philippines, as a subspecies of *H. bicolor*, and maintained the status of *H. bicolor macrobullatus* (Hill, 1963). Thus, *H. bicolor*, as newly defined by Hill (1963), ranged from southern India through mainland and insular Southeast Asia to the Philippines and Sulawesi. Once Hill (1963) had synonymized *H. pomona* and *H. gentilis* with *H. bicolor* to rectify what he thought was a mistake by Tate (1941), he was left with a large group of medium-sized bats that previously had been part of *H. bicolor* (Dobson, 1878; Lawrence, 1939; Laurie and Hill, 1954). Hill (1963) declared *H. ater* Templeton, 1848, a species described from Sri Lanka, as the next available name for what Andersen (1918) had defined as *H. bicolor*. Thus, Hill (1963) synonymized all medium-sized *bicolor*-like forms in insular Southeast Asia, New Guinea, and Australia as subspecies of *H. ater*.

Upon further examination of the *H. bicolor* complex, Hill *et al*. (1986) found *H. b. macrobullatus* distinct enough to warrant elevation to specific status, and discovered that *H. bicolor* in peninsular Malaysia and southern Thailand consisted of two morphologically distinct species: *H. pomona* and *H. bicolor*. With the removal of *pomona* (including *gentilis* and *sinensis*) and *macrobullatus*, *H. bicolor* (including *atrox* and *major*) was restricted to peninsular Thailand, the Malay peninsula, Sumatra, Java, Borneo, and the Philippines (*H. b. erigens*). Kitchener *et al*. (1996) studied morphological variation in *H. bicolor* in some of the Lesser Sunda Islands and extended the range of *H. bicolor* to include Timor, Roti, Savu, Sambu, Sambawa, and Selaru, describing three new subspecies of *H. bicolor* from these islands.

Based on morphology, a more recent taxonomic review of *H. bicolor* and *H. pomona* in Thailand suggested that *H. bicolor*-131 was conspecific with the lectotype of *H. bicolor* and thus should retain the name *H. bicolor* (Douangboubpha *et al*., 2010). The authors also suggested that *H. bicolor*-142 might represent an undescribed species but could not rule out conspecific status with either *H. atrox* or *H. javanicus.* Although the *H. atrox* holotype was generally larger than Thai *H. bicolor*-142 and did not cluster with either of the *H. bicolor* phonic types in multivariate analysis, *H. bicolor*-142 was provisionally referred to the earliest available name within Asian mainland distribution, *H. atrox* (Douangboubpha *et al*., 2010)

The goal of the current study was to resolve the taxonomic status of *H. bicolor*-131 and *H. bicolor*-142. To do so we analyzed morphological, genetic and acoustic data from the two phonic types sampled at multiple localities on the Malay peninsula and Borneo, together with other closely related lineages in the *bicolor* species group. Our study builds from that of Douangboubpha *et al*. (2010) in two important ways. First, our morphometric analyses include cranial measurements, collected by SWM, from all available type specimens in the *H. bicolor*

complex. Second, inclusion of molecular data provides an evolutionary context for our taxonomic evaluation of *H. bicolor*-131 and *H. bicolor*-142, and independent validation of field identifications based on echolocation call frequency. We find strong support for retention of the 131 kHz phonic type as *H. bicolor* but determine that *H. bicolor*-142 is not conspecific with *H. atrox* or any other previously named species. We therefore provide a complete description for a new species in the *bicolor* group.

Materials and Methods

Study Sites and Sampling

Bat surveys were conducted at caves in peninsular Malaysia and Southern Thailand, and at several forest sites in Krau Wildlife Reserve (KWR), and Kuala Atok in Taman Negara, relatively pristine and extensive lowland rainforests in central peninsular Malaysia (Fig. 1). Surveys took place June–August 2002, February 2003–September 2004, August 2006 and May 2008. Sampling in KWR was conducted in conjunction with and followed the sampling regime of the Malaysian Bat Conservation Research Unit (MBCRU; Kingston *et al*., 2006). Bats were captured in four-bank harp traps (Francis, 1989) set along trails in forested areas and at the openings to caves. Captured individuals were identified to species following Medway (1982), Payne and Francis (1985), and Kingston *et al*. (2006). Juveniles were distinguished from adults based on the presence of cartilaginous epiphyseal growth-plates in the phalanges (Anthony, 1988; Brunet-Rossinni and Wilkinson, 2009) and were excluded from all analyses. Sex and reproductive condition were noted (Racey, 2009), and pregnant bats were eliminated from analyses of body mass. Individuals were weighed with Pesola spring scales (Pesola AG, Switzerland) to the nearest 0.1 g, lengths of forearm and tibia were measured using dial calipers to the nearest 0.1 mm, and ear height and tail length were measured with a metal ruler to the nearest 0.5 mm. Tissues samples or wing biopsies were extracted from these individuals and preserved in 95% ethanol for genetic analyses. Selected specimens were prepared as museum vouchers. Animals were handled following the standards of the American Society of Mammalogists (Sikes *et al*., 2016), the Institutional Animal Care and Use Committee of Boston University (File No. 01-106), and the Texas Tech Animal Care and Use Committee (Permit No. 02217-02). Voucher specimens and duplicates of tissue samples were deposited in the Natural Science Research Laboratory, Museum of Texas Tech University (NSRL-TTU), Natural History Museum

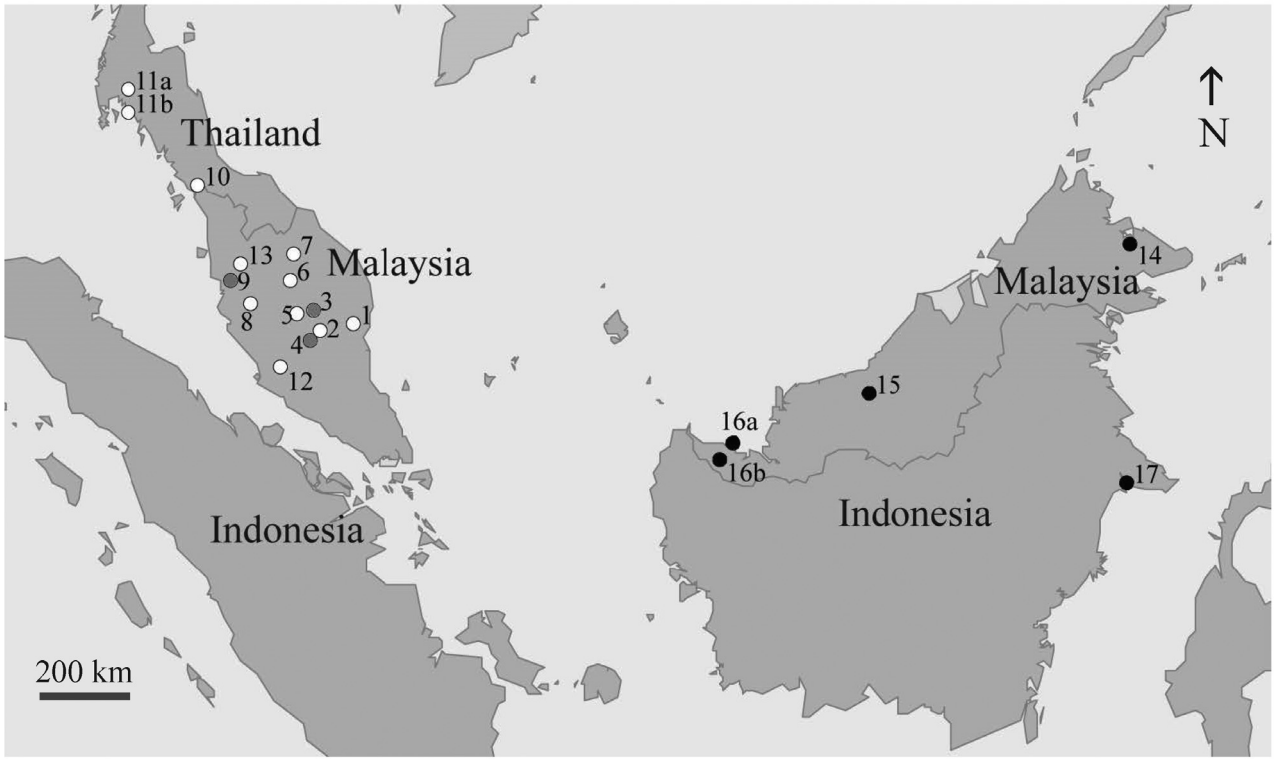

Fig. 1. Sampling localities in peninsular Malaysia (sites 1–10 and 12–13), Thailand (site 11) and Borneo (sites 14–17): 1, Pahang: Kuantan; 2, Pahang: Kota Gelanggi; 3, Pahang: Kuala Atok; 4, Pahang: Krau Wildlife Reserve; 5, Pahang: Kuala Lipis; 6, Kelantan: Gua Musang; 7, Kelantan: Dabong; 8, Perak: Ipoh; 9, Perak: Taiping; 10, Perlis: Perlis State Park; 11a, Krabi: Ao Luk; 11b, Krabi: Ao Nang; 12, Selangor: Ampang Reservoir; 13, Perak: Lenggong; 14, Sabah: Gomantong; 15, Sarawak: Ulu Kakas; 16a, Sarawak: Bako National Park; 16b, Sarawak: Bau; and 17, East Kalimantan. Circle color indicates capture sites for the two phonic types of *Hipposideros bicolor*: black, only *H. bicolor* (=*H. bicolor*-131), open, only *H. kunzi* sp. nov. (=*H. bicolor*-142), grey both species. The map was created using www.planiglobe.com

of Universiti Malaysia Sarawak (UNIMAS), Universiti Kebangsaan Malaysia (UKM), and Institute of Biological Diversity, Bukit Rengit, Pahang (IBD).

Echolocation Analyses

Echolocation calls of hipposiderid bats are dominated by a constant frequency (CF) component, followed by a frequency modulated (FM) tail. The frequency of the CF component of motionless bats provides an estimate of the resting frequency, and can be used in species identification (Hiryu *et al*., 2005). Echolocation calls of hand-held bats were recorded using a Pettersson D960 bat detector or an Ultra Sound Advice (USA) S-25 bat detector linked to a USA S-350 digital signal processor. Time-expanded (10× or 20×) output was recorded on a Sony WM-D6C Walkman cassette recorder and later downloaded to a computer. For each individual, the mean frequency of the CF component was calculated from six randomly selected calls using power spectra in BatSound Pro 3.30 (Pettersson Elektronik AB).

Wing and Skull Morphology

Differences in wing morphology can influence flight performance; we therefore assessed wing morphology of the two putative species of *H. bicolor* by taking digital photographs of bats with their right wing extended to the side with the propatagium forming a 90º angle with the body. A 10-cm line was included as a measure of scale. Wingspan, wing area, and the lengths and areas of the arm-wing and hand-wing were measured using ImageJ software (U.S. National Institutes of Health, Bethesda, Maryland, USA, https://imagej.nih.gov/ij/), and aspect ratio, wing loading, and wingtip index were calculated following Norberg and Rayner (1987).

Skulls were extracted from a total of 79 voucher specimens of *H. bicolor*, including both phonic types, and closely related species (*H. cineraceus*, *H. halophyllus*, and *H. pomona* — see Appendix). Specimens were deposited at Universiti Kebangsaan Malaysia (Bangi, Selangor, Malaysia). An additional 51 skulls from museum collections, including type specimens of *H. bicolor* and closely related taxa (including type specimens of *H. gentilis atrox*), were measured (Appendix). Six dental and 14 cranial characters were measured to the nearest 0.1 mm under a dissecting microscope fitted with an ocular micrometer (which was calibrated using the same ruler throughout the study), and two skull length characters (GSL and CCL) were measured to the nearest 0.01 mm with Mitutoyo digital calipers (Mitutoyo, Kawasaki, Japan). All cranio-dental measurements were recorded by the same specimen (SWM). Characters were defined as follows (see Bates and Harrison, 1997): greatest antero-posterior length of the skull (GSL); condylo-canine length from an exoccipital condyle to the anterior of a canine (CCL); height of the braincase at the highest point including tympanic bullae and the sagittal crest (HB); rostral height at the highest point of the rostrum excluding teeth (RH); greatest width across the zygomatic arches (ZW); greatest width across the mastoids (MW); greatest width across the dorsal surface of the rostrum (RW); narrowest width at the interorbital constriction (IOW); palatal width taken across the third upper molars at the widest part including the molars (M^3M^3); anterior width of the rostrum including the canines (CC); length of the hard palate (PL); two measures of the length of the maxillary toothrow (CM^3 and M^1M^3) measured from the alveolus of the upper canine (C) and first molar (M^1), respectively, to the back of the crown of the third upper molar (M^3); length of the upper canine (LUC); length of the tympanic bulla (LTB); transverse diameter of the exposed part of the cochlea (WCC); length of the dentary (DL); two measures of the mandibular toothrow (CM_3 and M_1M_3), length of the lower toothrow from the canine (C), from the first molar (M_1), and to the back of the crown of the last molar (M_3); length of the lower canine (CL); coronoid process height (CPH); condyle height (CDH). All 22 skull measurements were repeatable, with a coefficient of variance less than 0.05 based on 20 non-consecutive measures taken on one skull.

Genetic Analyses

Total genomic DNA was isolated from ethanol preserved wing or organ tissue using DNeasy Tissue Kits (Qiagen) and associated protocols. We sequenced 509 base pairs (bp) of the NADH dehydrogenase subunit 2 (ND2) gene, following the protocols described in Murray *et al*. (2012). The likelihood of amplifying nuclear copies of ND2 was reduced by using degenerate primers (Sorenson *et al*., 1999), and there were no insertions, deletions or stop codons in the translated sequences. Sequences were edited and aligned by eye using CodonCode Aligner v.1.5.2 (CodonCode Corporation).

The General Time Reversible (GTR) model of sequence evolution with gamma-distributed rate variation across sites (G) and a proportion of invariable sites (I) had the best Akaike information criterion (AIC) score as estimated in Modeltest v. 3.7 (Posada and Crandall, 1998) and was used in PAUP*4.0b10 (Swofford, 2003) to calculate the corrected genetic distances. We inferred a phylogenetic hypothesis by implementing the GTR+G+I model in MrBayes 3.1.2 (Ronquist and Huelsenbeck, 2003), with parameters estimated during the analysis. Two sets of four chains were run for two million generations, sampling trees every 100 generations. The two sets of chains converged and the first 25% of samples were excluded as the burnin. This analysis was repeated two additional times with different, randomly selected starting trees to ensure that the results were not stalled on a local peak. There were no differences in tree topology among the three replicates, therefore a consensus tree and mean posterior probabilities were calculated across the three runs.

To better resolve relationships between the two phonic types, the ingroup included representative lineages from three closely related taxa (*H. ater*, *H. cineraceus*, *H. pomona*), and a lineage from the Philippines, currently assigned to *H. bicolor* (Murray *et al*., 2012). *Hipposideros cervinus* and *H. armiger* were used as outgroup taxa, because they represent the two clades that form a basal polytomy with *H. bicolor* and its allies (Murray *et al*., 2012). To examine population level relationships within the two putative species of *H. bicolor*, TCS (Clement *et al*., 2000) was used to infer statistical parsimony networks.

Karyotype Preparations

Karyotype slides were prepared following the karyotype preparation steps under field conditions as described in Baker *et al*. (2003). Slides were examined using an Olympus epi-fluorescence microscope BX51 and photographed using an Applied Imaging® camera. Karyotype images were arranged using the Genus™ System 3.1 (Applied Imaging Systems, San Jose, California). Karyotypes were described by diploid and fundamental numbers.

Statistical Analyses

Echolocation call frequency, measures of external morphology (body mass, lengths of forearm, tibia, tail and ear height), wing variables, and skull characters were tested for sexual dimorphism using either *t*-tests with a Bonferroni correction for multiple tests or general linear models (GLM). To examine interspecific differences in morphology, multivariate GLM analyses with Tukey's post-hoc tests were used for each dataset (i.e., external, wing and skull morphologies, and echolocation call frequency). Analyses for external and wing morphology, and echolocation call frequency only included individuals from peninsular Malaysia. Forward stepwise discriminant function analyses (DFA) were performed to determine how well the putative *H. bicolor* species could be differentiated using the characters we measured, and to find characters that could be used for field identification. As DFA is an a priori test, individuals were first assigned to species based on echolocation frequency and/or genetic data. Leave-one-out classification was used to assess the performance of the selected characters in predicting group membership. For datasets with sufficiently large sample sizes, 70% of the individuals were randomly selected and used to calculate the DFA, and the remaining 30% of the samples were used as an independent test of the DFA. There were not enough samples to use an independent cross-validation in the skull and wing DFAs, and in these cases the same data were used to create the DFA and test it. Using the results of the DFAs, the putative species of *H. bicolor* were compared to type material to assess their taxonomic status. All statistical tests were performed using SPSS for Windows 15.0 with a type I error rate of $\alpha = 0.05$, unless stated otherwise. All means are presented with plus or minus one standard deviation, and the range.

Results

Genetic Analyses

The ND2 gene was sequenced for 206 individuals. Phylogenetic hypotheses were inferred for a reduced dataset that included all 61 unique haplotypes (Fig. 2). Fourteen of these haplotypes were previously published as part of a phylogenetic analysis that included a larger taxonomic sample of Southeast Asian hipposiderids (Murray *et al*., 2012), the remainder are new to this study (see Appendix for GenBank accession numbers). All ingroup taxa were polyphyletic: *H. ater*, *H. bicolor*, and *H. cineraceus* were polyphyletic with respect to each other, and *H. bicolor*-131 and -142 were not sister taxa (Fig. 2). Individuals of *H. bicolor* fell into three distinct clades (Fig. 2): the specimen from the Philippines was most closely related to individuals identified as *H. ater* from Sabah (Borneo) and East Kalimantan (Borneo), and the two phonic types of *H. bicolor* from Malaysia were recovered in reciprocally monophyletic clades (Fig. 2). There was 12.4–13.2% uncorrected sequence divergence between the Malaysian and Philippine specimens, and 7.1–10.2% divergence among the two main groups of *H. bicolor* from Malaysia (Table 1).

Within *H. bicolor*-131, there was weak support (posterior probability [pp] = 0.80) for a clade containing all the individuals from Borneo, including those from Sabah, Sarawak, and East Kalimantan. Although no echolocation data were available for the Borneo samples, lengths of forearm and appearance were consistent with those of *H. bicolor*-131 from peninsular Malaysia (Khan *et al*., 2007). The *H. bicolor*-131 individuals from peninsular Malaysia formed two clades, with a weakly-supported sister relationship (pp = 0.78). The first clade, referred to as the Taiping group, included individuals from Taiping, Perak state (Fig. 1: site 9) and Kuala Atok, Pahang state (Fig. 1: site 3), and the second clade, the KWR group, consisted of individuals captured in Krau Wildlife Reserve, Pahang (Fig. 1: site 4) and Kuala Atok. The uncorrected genetic distances within each of the three groups (Borneo, Taiping, and KWR) ranged from 0 to 2.4%, while the distances between the groups ranged from 3.7 to 5.1% (Table 1). There were 15 different haplotypes in the *H. bicolor*-131 clade: five relatively similar haplotypes among 34 individuals from KWR (M1-M4) and Kuala Atok (M7), three Taiping haplotypes (two from Taiping, M5 and M6, and one from Kuala Atok, M8) among four individuals, and seven haplotypes among 17 individuals from Borneo (B1-B7). The statistical parsimony analysis with 95% connection limit recovered three separate networks, corresponding to the Taiping, KWR and Borneo groups (Fig. 3, solid lines). When the connection limit was relaxed, the KWR and Borneo networks were connected with 15 steps between them, and the Taiping and Borneo groups were connected with 17 steps (Fig. 3, dashed lines).

The second major clade comprised individuals identified as *H. bicolor*-142 and *H. cineraceus*-B using morphological characters. The placement of *H. cineraceus*-B as a basal member of the *H. bicolor*-142 clade was well-supported (pp = 1.00; Fig. 2). There was 4.7 – 7.1% divergence between these two taxa (Table 1). Within *H. bicolor*-142, we recovered three clades (Fig. 2). The first group had the smallest genetic distance to *H. cineraceus*-B (4.7–4.9% uncorrected; Table 1) and included individuals from two relatively close sites in Southern Thailand (Fig. 1: sites 11a & 11b). The Perlis and Malay groups formed a moderately-supported clade (pp = 0.92; Fig. 2), with 2.2 to 3.1% sequence divergence between them (Table 1). There was weak support for the Perlis group (pp = 0.86; Fig. 2), which

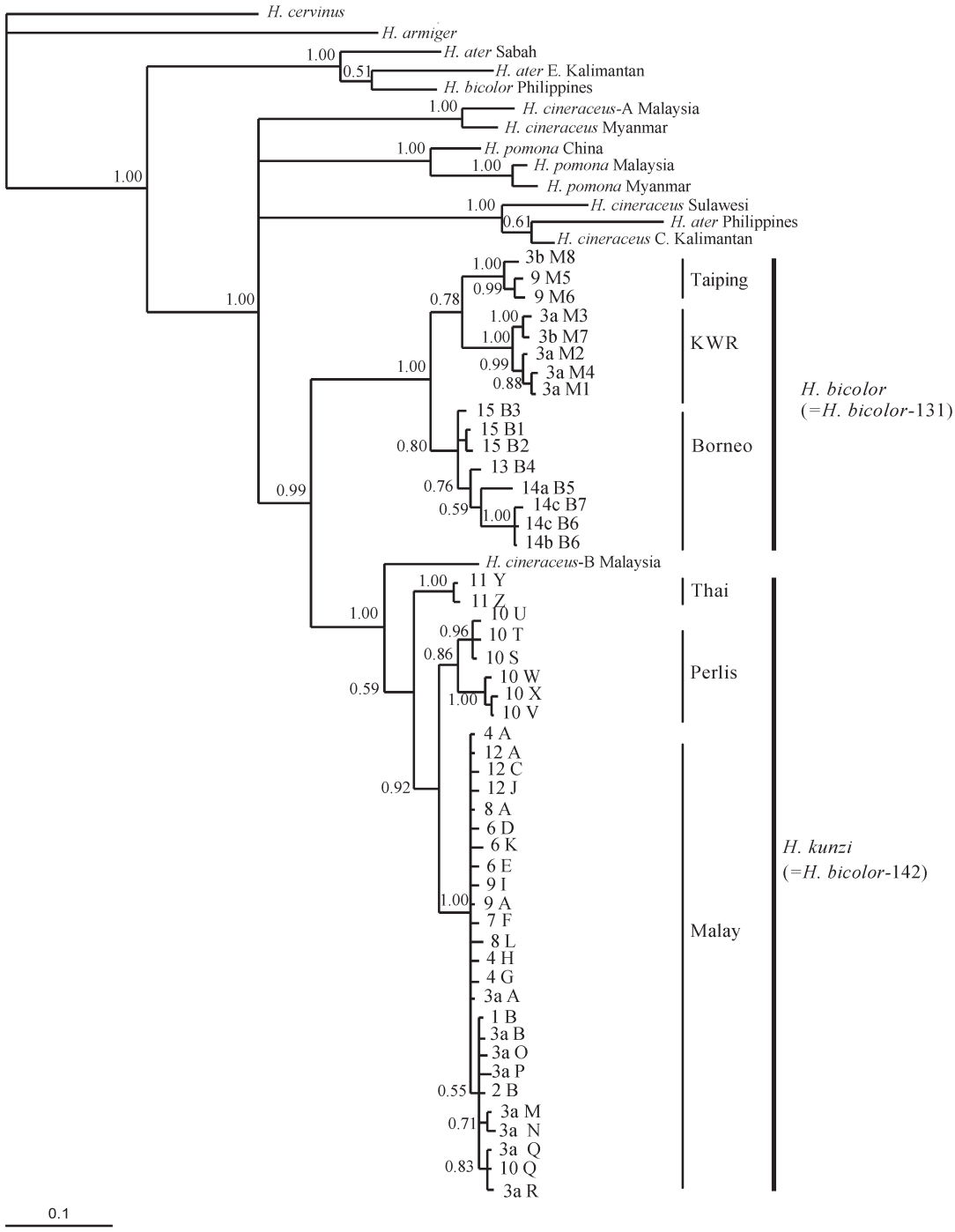

FIG. 2. Phylogram generated from a Bayesian analysis using the GTR+G+I model of nucleotide evolution. Branch lengths are proportional to the number of substitutions as indicated by the scale bar. Tip labels for the different species of *H. bicolor* include the capture site (Fig. 1) followed by the haplotype (Figs. 3 and 4). Posterior probabilities (pp) are next to the nodes

included *H. bicolor*-142 individuals from Perlis state in northern Malaysia, near the Thai border (Fig. 1: site 10). The Malay group comprised individuals from all 11 localities sampled in peninsular Malaysia, including one individual from Perlis state, and was well-supported (pp = 1.00). There was 3.3–4.7% uncorrected divergence between the Perlis and Thai groups and 2.9–3.9% divergence between the Malay and Thai groups (Table 1).

The uncorrected genetic distances within each of the three *H. bicolor*-142 groups ranged from 0–2.0%, with the highest divergence between haplotypes in the two Perlis subclades (Table 1 and Fig. 2). Despite the relatively large size and wide

TABLE 1. Genetic distances among different populations of *H. bicolor* (=*H. bicolor*-131), *H. kunzi* (=*H. bicolor*-142) and *H. cineraceus*-B. Below the diagonal are the uncorrected genetic distances, along the diagonal (in bold) are uncorrected distances within each group, and above the diagonal are corrected distances using the GTR+G+I model of evolution. Population names refer to taxa or clades in Fig. 2

Population	*H. bicolor* KWR	*H. bicolor* Taiping	*H. bicolor* Borneo	*H. kunzi* Thai	*H. kunzi* Perlis	*H. kunzi* Malay	*H. cineraceus*-B
131 KWR	**0.2–1.4**	5.7–6.3	4.4–6.4	12.4–13.8	11.5–13.7	12.8–15.7	14.6–15.4
131 Taiping	4.7–5.1	**0.6**	5.1–5.6	13.6–14.2	12.8–14.0	13.9–16.2	14.7–14.9
131 Borneo	3.7–5.1	4.3–4.7	**0.2–2.4**	10.5–11.9	9.7–12.0	9.3–12.8	12.2–13.9
142 Thai	8.6–9.2	9.0–9.4	7.7–8.4	**0.2**	5.9–6.2	3.4–4.8	5.9–6.2
142 Perlis	8.3–9.2	8.8–9.4	7.3–8.4	3.3–4.7	**0.2–2.0**	2.4–3.9	7.7–9.8
142 Malay	8.8–10.0	9.2–10.2	7.1–8.8	2.9–3.9	2.2–3.1	**0.0–1.0**	7.8–9.4
H. cineraceus-B	9.6–10.0	9.8–10.0	8.6–9.5	4.7–4.9	5.9–7.1	5.9–6.7	–

geographic distribution of the Malay group there was little structure in this clade (Fig. 2), with a maximum of 1% sequence divergence between haplotypes (Table 1). In all, there were 26 different haplotypes within the *H. bicolor*-142 clade: two haplotypes among seven individuals from the Thai group, six haplotypes among 13 individuals in the Perlis group, and 18 haplotypes among 117 individuals comprising the Malay group. The statistical parsimony analysis connected the Malay and Perlis clades at a connection limit of 93% (Fig. 4, solid lines). The Thai group was 15 steps removed from the Malay group with a connection limit below 90% (Fig. 4, dashed line). Haplotype A in Fig. 4 was designated as the most basal haplotype in this analysis.

Echolocation

Call frequency was recorded for 1,008 adult individuals in the *H. bicolor* complex from peninsular Malaysia. Echolocation data were not available from individuals captured in Taiping, Kuala Atok, or Borneo. The relationship between length of forearm and variation in echolocation call frequency for *H. bicolor*-131 and *H. bicolor*-142 is shown in

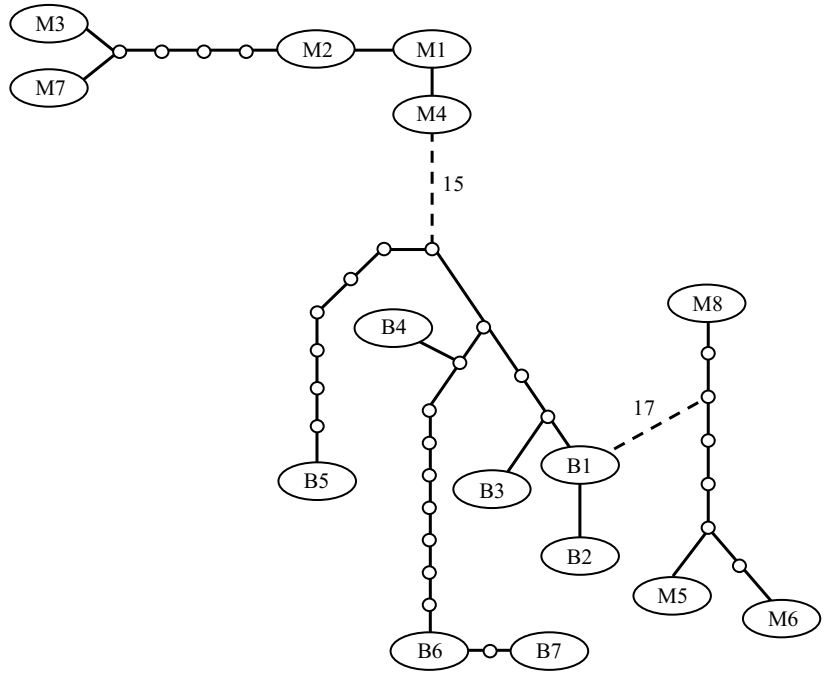

FIG. 3. Results of the statistical parsimony analysis for *H. bicolor* (=*H. bicolor*-131). Solid lines are equivalent to one base pair difference, and dashed lines represent connections between networks when the limits are relaxed. M haplotypes are from peninsular Malaysia (M1-4: Krau Wildlife Reserve, M5-6: Taiping, and M7-8: Kuala Atok), and B haplotypes are from Borneo (B1-3: East Kalimantan, B4: Sabah, and B5-7: Sarawak)

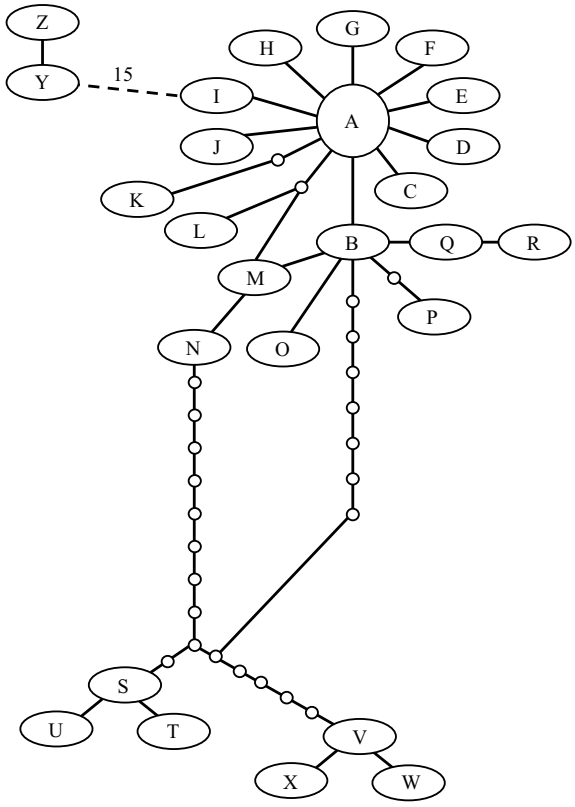

FIG. 4. Results of the statistical parsimony analysis for *H. kunzi* sp. nov. (=*H. bicolor*-142) recovered two groups, separated by the dashed line (15 steps). Solid lines represent one base pair change. Haplotypes Z and Y are from southern Thailand, haplotypes S, T, U, V, W, and X represent the Perlis group, and all other haplotypes are part of the Malay group. Haplotype A was determined to be the most basal in this analysis

Fig. 5. While the phonic types formed two distinct clusters, a fraction of calls fell in a band of overlap between 134 and 137 kHz (Fig. 5). Thirty-one of these intermediate calls (filled circles in Fig. 5) did not have associated genetic data and therefore could not be assigned to either phonic type and were not included in any further analyses. With these samples excluded, *H. bicolor*-142 and *H. bicolor*-131 had mean call frequencies of 143.1 ± 2.0 kHz (ranging from 135.8–147.5 kHz; n = 842 individuals) and 131.8 ± 2.0 kHz (ranging from 124.9–135.8, n = 136 — Table 2), respectively. Within *H. bicolor*-142, females (n = 403) had significantly lower echolocation calls (t = -4.31, *d.f.* = 842, $P < 0.001$; mean = 142.8 ± 2.2 kHz) compared to males (mean = 143.4 ± 1.9 kHz; n = 439 — Table 2). In contrast, female *H. bicolor*-131 (n = 75) had significantly higher echolocation calls (t = 4.65, *d.f.* = 134, $P < 0.001$; mean = 132.4 ± 1.4 kHz) compared to males (mean = 131.0 ± 2.2 kHz; n = 61).

Morphometric Comparisons within and between H. bicolor-*131 and* H. bicolor-*142*

External morphology

Basic measures of external morphology and body mass (Table 2) were collected from a total of 866 and 145 adult individuals from peninsular Malaysia unambiguously identified as *H. bicolor*-142 and *H. bicolor*-131, respectively, based on echolocation and/or genetic data. Five of these variables were sexually dimorphic within phonic type (Bonferroni-corrected α = 0.004). Female *H. bicolor*-142 had significantly longer forearms (t = 11.93, *d.f.* = 864, $P < 0.001$), tails (t = 8.86, *d.f.* = 719, $P < 0.001$), and ears (t = 3.35, *d.f.* = 666, P = 0.001 — Table 2) compared to males. Likewise, female *H. bicolor*-131 had significantly longer forearms (t = 8.28, *d.f.* = 141, $P < 0.001$), tibias (t = 4.30, *d.f.* = 129, $P < 0.001$), tails (t = 5.18, *d.f.* = 129, $P < 0.001$), and heavier body masses (t = 4.77, *d.f.* = 122, P = 0.001 — Table 2) compared to males.

Given these sex differences in size and echolocation call frequency (see above), univariate GLM analyses were run with phonic type split by sex. Body mass ($F_{3, 926}$ = 5.1, P = 0.002), echolocation call frequency ($F_{3, 975}$ = 1,382.7, $P < 0.001$), lengths of forearm ($F_{3, 1004}$ = 417.1, $P < 0.001$), tibia

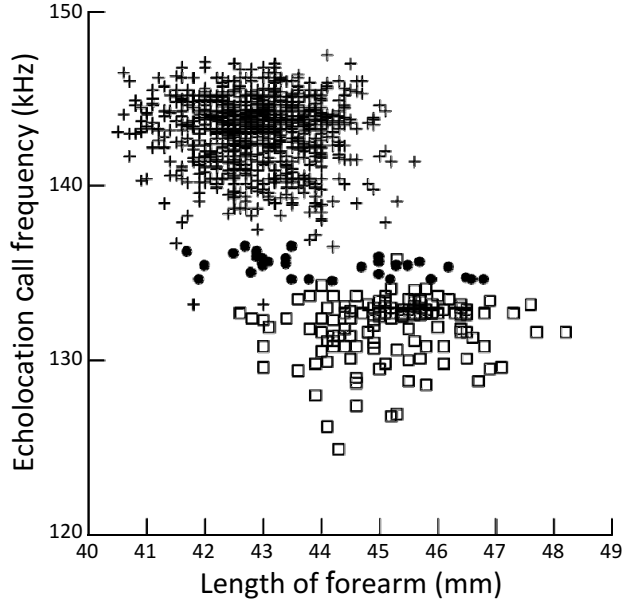

FIG. 5. Distribution of echolocation call frequencies and lengths of forearm for all *H. bicolor* captured in peninsular Malaysia for which echolocation call data were available. *H. bicolor* (=*H. bicolor*-131; open squares), *H. kunzi* sp. nov. (=*H. bicolor*-142; crosses), and unidentified individuals with intermediate call frequency (solid circles) were included

TABLE 2. Mean values for external and wing morphology with standard deviation and sample size (in parentheses) for *H. bicolor* (=*H. bicolor*-131) and *H. kunzi* (*H. bicolor*-142) captured in peninsular Malaysia (not including bats from Taiping and Kuala Atok). Ranges are also presented for external morphology and echolocation. Values for *H. cineraceus*-B are included for comparison because of this lineage's close phylogenetic relationship with *H. kunzi*, but were not included in statistical analyses. The results of univariate GLM analyses for an effect of species on external measurements and echolocation call frequency with phonic type split by sex are given: * — $P < 0.05$, ** — $P < 0.01$, and *** — $P < 0.001$. For the wing morphology data, the results of a GLM analysis with the sexes pooled, species as a fixed factor and length of forearm as a covariate are also shown. Differences between males and females within each phonic type were evaluated using *t*-tests; $\alpha = 0.004$ after Bonferroni correction

Variable	*H. bicolor* KWR	*H. kunzi*	*H. cineraceus*-B
Forearm length (mm)***	45.3 ± 1.0 (143)	42.9 ± 0.9 (864)	39.3 (1)
Range	43.0–48.2	38.8–45.6	
♀♀	45.8 ± 0.8 (76)***	43.3 ± 0.8 (414)***	
♂♂	44.7 ± 0.8 (67)	42.6 ± 0.8 (450)	
Tibia length (mm)***	20.5 ± 0.6 (131)	18.8 ± 0.5 (742)	17.2 (1)
Range	18.7–22.1	17.1–20.4	
♀♀	20.7 ± 0.6 (67)***	18.8 ± 0.5 (363)	
♂♂	20.3 ± 0.5 (64)	18.8 ± 0.5 (379)	
Tail length (mm)***	31.2 ± 2.1 (131)	28.7 ± 1.8 (719)	34.0 (1)
Range	26.0–35.0	21.0–34.0	
♀♀	32.0 ± 1.8 (68)***	29.3 ± 1.6 (356)***	
♂♂	30.2 ± 2.1 (63)	28.2 ± 1.7 (363)	
Ear height (mm)***	18.2 ± 0.7 (132)	17.6 ± 0.6 (666)	16.0 (1)
Range	15.1–20.5	15.0–19.5	
♀♀	18.2 ± 0.8 (66)	17.7 ± 0.6 (315)***	
♂♂	18.1 ± 0.7 (66)	17.5 ± 0.6 (351)	
Body mass (g)**	8.6 ± 0.8 (124)	8.5 ± 0.9 (805)	6.0 (1)
Range	6.8–10.8	5.8–12.0	
♀♀	8.9 ± 0.8 (62)***	8.5 ± 1.0 (357)	
♂♂	8.3 ± 0.7 (62)	8.5 ± 0.9 (448)	
Call frequency (kHz)***	131.8 ± 2.0 (136)	143.1 ± 2.0 (842)	144.0†
Range	124.9–135.8	135.8–147.5	
♀♀	132.4 ± 1.4 (75)***	142.8 ± 2.0 (403)***	
♂♂	131.0 ± 2.2 (61)	143.4 ± 1.9 (439)	
Wing area (m^2)	0.0135 ± 0.0008	0.0121 ± 0.0007	
♀♀	0.0139 ± 0.0007*	0.0123 ± 0.0007	
♂♂	0.0132 ± 0.0007	0.0119 ± 0.0007	
Arm-Wing area (m^2)**	0.0033 ± 0.0002	0.0031 ± 0.0002	
♀♀	0.0034 ± 0.0003	0.0032 ± 0.0002***	
♂♂	0.0033 ± 0.0002	0.0030 ± 0.0002	
Hand-Wing area (m^2)***	0.0024 ± 0.0001	0.0021 ± 0.0001	
♀♀	0.0025 ± 0.0001	0.0021 ± 0.0001	
♂♂	0.0024 ± 0.0001	0.0021 ± 0.0001	
Wing span (m)	0.2863 ± 0.0088	0.2736 ± 0.0088	
♀♀	0.2896 ± 0.0079	0.2758 ± 0.0076	
♂♂	0.2837 ± 0.0088	0.2715 ± 0.0092	
Arm-Wing length (m)**	0.0572 ± 0.0020	0.0549 ± 0.0020	
♀♀	0.0577 ± 0.0018	0.0556 ± 0.0018**	
♂♂	0.0567 ± 0.0021	0.0542 ± 0.0019	
Hand-Wing length (m)*	0.0654 ± 0.0026	0.0629 ± 0.0024	
♀♀	0.0664 ± 0.0019	0.0633 ± 0.0023	
♂♂	0.0646 ± 0.0029	0.0624 ± 0.0023	
Wing loading (N/m^2)***	6.19 ± 0.56	6.74 ± 0.76	
♀♀	6.32 ± 0.57	6.65 ± 0.76**	
♂♂	6.10 ± 0.54	6.84 ± 0.75	
Aspect ratio*	6.08 ± 0.23	6.18 ± 0.23	
♀♀	6.04 ± 0.21	6.17 ± 0.22	
♂♂	6.11 ± 0.24	6.19 ± 0.24	
Tip index***	1.76 ± 0.30	1.44 ± 0.28	
♀♀	1.72 ± 0.32	1.39 ± 0.24**	
♂♂	1.80 ± 0.29	1.49 ± 0.32	

† — Data from Kingston *et al*. (2000)

($F_{3, 869}$ = 422.6, P < 0.001), tail ($F_{3, 847}$ = 111.3, P < 0.001), and ear height ($F_{3, 795}$ = 37.0, P < 0.001) were significantly different across these four groups. Echolocation call frequency explained the largest amount of variance among male and female *H. bicolor*-131 and *H. bicolor*-142 (r^2 = 0.81), followed by lengths of tibia (r^2 = 0.59) and forearm (r^2 = 0.56). Length of tail (r^2 = 0.28) and ear height (r^2 = 0.12) explained little of the variance and mass accounted for the least amount of variance (r^2 = 0.02). *Hipposideros bicolor*-131 females were significantly heavier than the other three groups (Tukey's post-hoc test, P < 0.01) but there were no differences in mass among male and female *H. bicolor*-142 and male *H. bicolor*-131 (P > 0.05 — Table 2). Length of forearm, length of tail, and echolocation call frequency were all significantly different across the four groups (all P < 0.001). Females were larger than males in both species and individuals of *H. bicolor*-131 were larger and had lower echolocation call frequencies than individuals of *H. bicolor*-142. There was no difference between male and female *H. bicolor*-142 for length of tibia (P > 0.1), but there were significant differences among the other groups (P < 0.001), with female *H. bicolor*-131 having the longest tibias followed by male *H. bicolor*-131 and then *H. bicolor*-142. There were significant differences in ear height among male *H. bicolor*-142, female *H. bicolor*-142 and *H. bicolor*-131 (P < 0.01), but there was no significant difference in ear height between the sexes of *H. bicolor*-131 (P > 0.1 — Table 2).

While the two *H. bicolor* phonic types are defined by difference in echolocation call frequency, not all field workers have access to recording equipment and echolocation call data cannot be collected from museum specimens. Therefore, we conducted a discriminant function analysis (DFA) to determine whether *H. bicolor*-142 and *H. bicolor*-131 could be identified correctly using lengths of forearm and tibia, measurements that are easily collected from both live bats and museum specimens. The canonical coefficients for lengths of tibia and forearm were 0.771 and 0.333, respectively. The function at the group centroid was 2.909 for *H. bicolor*-131 and -0.510 for *H. bicolor*-142. There was some overlap in the DFA scores for the two species, but a total of 96.8% of *H. bicolor*-131 and 96.2% of *H. bicolor*-142 were identified correctly, with four and 21 individuals misclassified, respectively. Classification was slightly worse in the independent validation, with 91.9% of *H. bicolor*-131 and 95.3% of *H. bicolor*-142 identified correctly.

Wing morphology

We removed the effect of forearm size, a potentially confounding variable, by using it as a covariate in the multivariate GLM analysis. Female *H. bicolor*-142 had significantly larger arm-wing area ($F_{1, 226}$ = 13.2, P < 0.001) and length ($F_{1, 226}$ = 9.9, P = 0.002) and significantly lower wing loading ($F_{1, 226}$ = 7.2, P = 0.008) and tip index ($F_{1, 226}$ = 6.9, P = 0.009) than males (Table 2). Wing area was the only sexually dimorphic character in *H. bicolor*-131 ($F_{1, 56}$ = 4.24, P = 0.04), with females having a larger wing area (Table 2).

We compared wing morphology between *H. bicolor*-131 and *H. bicolor*-142 using a GLM analysis with the sexes pooled, species as a fixed factor and length of forearm as a covariate. There was no difference between the two species for overall wing area ($F_{1, 283}$ = 0.84, P = 0.4) or wingspan ($F_{1, 283}$ = 1.25, P = 0.3), but *H. bicolor*-131 had significantly larger arm-wing area ($F_{1, 283}$ = 7.41, P = 0.007) and length ($F_{1, 283}$ = 8.18, P = 0.005) and hand-wing area ($F_{1, 283}$ = 28.14, P < 0.001) and length ($F_{1, 283}$ = 5.84, P = 0.02). *Hipposideros bicolor*-131 had a significantly lower wing loading ($F_{1, 283}$ = 23.75, P < 0.001), a more rounded wing-tip (higher tip index; $F_{1, 283}$ = 32.19; P < 0.001), and a slightly, but significantly, more rounded wing (lower aspect ratio; $F_{1, 283}$ = 5.59, P = 0.02) than *H. bicolor*-142.

Skull morphology

A total of 85 skulls (41 ♀♀ and 44 ♂♂) from eight different sites in peninsular Malaysia were measured for *H. bicolor*-142. In a GLM analysis with sex as a fixed factor, six out of 22 skull variables exhibited significant sexual size dimorphism. Males had significantly longer skulls (GSL: $F_{1, 84}$ = 6.9, P = 0.01) and dentaries (DL: $F_{1, 84}$ = 4.6, P = 0.04), although the length of the skull from the occipital condyle to the canines was not significantly different between the sexes (CCL: $F_{1, 84}$ = 2.1, P = 0.2). In addition, males had a significantly taller braincase (HB: $F_{1, 84}$ = 8.0, P = 0.006), wider rostrum at the canines including the canines (CC: $F_{1, 84}$ = 8.2, P = 0.005) and longer canines in both the lower (CL: $F_{1, 84}$ = 44.4, P < 0.001) and upper jaws (LUC: $F_{1, 84}$ = 19.9, P < 0.001). Fifteen skull variables exhibited significant intraspecific differences across study sites, but small sample sizes precluded any meaningful analyses (data not shown).

Complete skull data were available from 23 individuals of *H. bicolor*-131, 7 from Borneo (including individuals from Sarawak, Sabah, and East Kalimantan) and 16 from KWR in peninsular Malaysia

(Appendix). GLM analyses examining sexual size dimorphism within the Borneo and KWR samples demonstrated that females from KWR had wider rostra (RW: $F_{1, 15} = 5.4$, $P = 0.04$), palates (M^3M^3: $F_{1, 15} = 5.9$, $P = 0.03$), and cochlea (WCC: $F_{1, 15} = 5.3$, $P = 0.04$) than did males, and males had significantly taller canines in the lower jaw (CL: $F_{1, 15} = 5.9$, $P = 0.029$). There was no significant sexual dimorphism in skull characters for the Borneo sample ($P > 0.05$). There were, however, significant differences between KWR and Borneo: *H. bicolor*-131 from Borneo had longer toothrows in both the upper (CM^3: $F_{1, 22} = 6.5$, $P = 0.02$; M^1M^3: $F_{1, 22} = 43.0$, $P < 0.001$) and lower jaw (CM_3: $F_{1, 22} = 7.8$, $P = 0.01$; M_1M_3: $F_{1, 22} = 11.2$, $P = 0.003$), longer palates (PL: $F_{1, 22} = 5.8$, $P = 0.03$), taller rostra (RH: $F_{1, 22} = 6.0$, $P = 0.02$), narrower inter-orbital width (IOW: $F_{1, 22} = 4.6$, $P = 0.045$), and a shorter braincase (HB: $F_{1, 22} = 7.9$, $P = 0.01$) compared to individuals from KWR (Table 3).

In our combined analysis of the two phonic types, sample sizes for *H. bicolor*-131 were too small to treat sexes and sample sites separately. We compensated for unequal sampling across sexes and sites in *H. bicolor*-142 by selecting at random three individuals per sex, per site (Appendix). The majority of the skull characters in the multivariate GLM analysis were significantly different between the two phonic types (Table 3 and Fig. 6). Relative to *H. bicolor*-142, *H. bicolor*-131 had a significantly longer skull (GSL: $F_{1, 65} = 38.4$, $P < 0.001$; CCL: $F_{1, 65} = 47.9$, $P < 0.001$), longer toothrows in both the upper (CM^3: $F_{1, 65} = 6.0$, $P = 0.02$; M^1M^3: $F_{1, 65} = 4.5$, $P = 0.04$) and lower jaws (CM_3: $F_{1, 65} = 4.6$, $P = 0.04$), a wider and taller rostrum (RW: $F_{1, 65} = 117.0$, $P < 0.001$; RH: $F_{1, 65} = 10.6$, $P = 0.002$), a wider post-orbital constriction (IOW: $F_{1, 65} = 57.1$, $P < 0.001$) and cochlea (WCC: $F_{1, 65} = 11.0$, $P = 0.001$), a narrower palate (CC: $F_{1, 65} = 9.3$, $P = 0.003$; M^3M^3: $F_{1, 64} = 40.3$, $P < 0.001$) and skull across the zygomatic arches (ZB: $F_{1, 64} = 19.0$, $P < 0.001$). *Hipposideros bicolor*-142 had significantly longer upper (LUC: $F_{1, 65} = 11.8$, $P = 0.001$) and lower canines (CL: $F_{1, 65} = 8.3$, $P = 0.005$), a longer palate (PL: $F_{1, 65} = 18.9$, $P = 0.004$), and a taller braincase (HB: $F_{1, 65} = 9.0$, $P = 0.004$) compared to *H. bicolor*-131.

Comparisons with Type Specimens

There are four *Hipposideros* species in Southeast Asia and the Indian subcontinent that overlap in body size and superficially resemble each other: *H. bicolor*, *H. pomona*, *H. macrobullatus*, and *H. fulvus*. The taxonomy of these species has a long history of entanglement (Andersen, 1918; Tate, 1941; Hill, 1963; Hill *et al*., 1986; Zubaid and Davison, 1987; Koopman, 1994; Bates and Harrison, 1997; Simmons 2005). However, *H. fulvus* is genetically distinct from *H. bicolor* (Murray *et al*., 2012) and is restricted to the Indian subcontinent, where *H. bicolor* does not occur, and thus was not included in the analysis. Because of similarities in external morphology between *H. bicolor*, *H. pomona*, and *H. macrobullatus* and the poor condition of many of the type specimens, we chose to only use skull morphology to assess whether any of the type specimens or their synonyms were conspecific with either of the phonic types of *H. bicolor* from peninsular Malaysia and Borneo. We note that, due to small sample sizes and limited geographic sampling for some of the species, a complete taxonomic revision of the *bicolor* group is beyond the scope of this study. Our main goal was to determine if any named forms were conspecific with the two phonic types of *H. bicolor*.

We performed a stepwise DFA using the 19 skull characters available for the incomplete skull of the *H. bicolor* lectotype (Naturalis, Leiden NL: RMNH 33654; GSL, RH, ZW, MW, RW, IOW, M^3M^3, CC, PL, CM^3, M^1M^3, LUC, WCC, DL, CM_3, M_1M_3, CL, CPH, and CDH) and included six species that occur in peninsular Malaysia and are morphologically similar and/or genetically closely related: *H. bicolor*-131 ($n = 24$, including individuals from peninsular Malaysia, Sarawak, Sabah, and East Kalimantan), *H. bicolor*-142 ($n = 48$), *H. cineraceus*-A ($n = 10$), *H. cineraceus*-B ($n = 1$), *H. halophyllus* ($n = 7$), and *H. pomona* ($n = 3$). A total of eight characters were retained with five functions (Table 4). The best separation among species was with functions one and two (Fig. 7A). Function one explained 79.5% of the variance and was a measure of dentary length (Table 4). Function two explained 17.6% of the variance and had high positive loadings for greatest skull length, width of the rostrum and inter-orbital width, and high negative loadings for zygomatic breadth and palate width (Table 4). The remaining three functions accounted for a total of 2.9% of the variance and therefore were not considered further. The three smaller species (*H. cineraceus*-A, *H. cineraceus*-B, and *H. halophyllus*) were separated from *H. pomona* and the two phonic types of *H. bicolor* along the first function, whereas separation within these two size groups was along the

TABLE 3. The means (in mm) ± SD, and ranges (in parentheses) for 22 skull variables (see Materials and Methods for descriptions) were compared between *H. kunzi* (=*H. bicolor*-142) and *H. bicolor* (=*H. bicolor*-131; including both KWR and Borneo individuals) using GLM analysis: * — $P < 0.05$, ** — $P < 0.01$, and *** — $P < 0.001$. The separate means for the two populations of *H. bicolor* (KWR and Borneo) are also shown. The measurements for the holotype and the paratypes for *H. kunzi* are included for comparison

Skull variables	*H. kunzi* (=*H. bicolor*-142) $n = 48$	*H. kunzi* holotype TTU108222	*H. kunzi* paratypes TTU108209/TTU108417	*H. bicolor* (=*H. bicolor*-131) $n = 23$	*H. bicolor* (=*H. bicolor*-131) KWR, $n = 16$	*H. bicolor* (=*H. bicolor*-131) Borneo, $n = 7$
GSL***	18.31 ± 0.33 (17.69–19.13)	18.47	18.57/18.69	18.83 ± 0.30 (18.38–19.57)	18.76 ± 0.25 (18.38–19.25)	18.97 ± 0.39 (18.59–19.57)
CCL***	15.56 ± 0.28 (15.08–16.30)	–	15.90/15.59	16.09 ± 0.34 (15.48–16.97)	16.00 ± 0.28 (15.48–16.67)	16.28 ± 0.41 (15.95–16.97)
CM^3*	6.3 ± 0.1 (6.1–6.6)	6.3	6.5/6.6	6.4 ± 0.1 (6.1–6.6)	6.4 ± 0.1 (6.1–6.5)	6.5 ± 0.1 (6.3–6.6)
M^1M^3	3.8 ± 0.1 (3.7–4.1)	3.9	4.0/4.1	3.9 ± 0.1 (3.7–4.2)	3.8 ± 0.1 (3.7–4.0)	4.0 ± 0.1 (4.0–4.2)
HB**	8.2 ± 0.2 (7.7–8.5)	7.7	7.8/7.9	8.0 ± 0.2 (7.7–8.4)	8.1 ± 0.2 (7.7–8.4)	7.8 ± 0.2 (7.7–8.3)
LUC***	2.4 ± 0.1 (2.1–2.7)	2.6	2.4/2.4	2.3 ± 0.1 (1.9–2.5)	2.3 ± 0.1 (1.9–2.5)	2.3 ± 0.2 (2.0–2.4)
RH**	4.4 ± 0.1 (4.1–4.7)	4.6	4.7/4.6	4.5 ± 0.1 (4.3–4.7)	4.5 ± 0.1 (4.3–4.7)	4.6 ± 0.1 (4.5–4.7)
MW	9.2 ± 0.2 (8.8–9.7)	9.2	9.4/9.2	9.3 ± 0.1 (9.0–9.6)	9.2 ± 0.1 (9.0–9.4)	9.3 ± 0.1 (9.1–9.6)
ZB***	9.5 ± 0.3 (9.0–10.1)	9.4	9.8/9.4	9.2 ± 0.1 (9.0–9.6)	9.2 ± 0.1 (9.0–9.4)	9.3 ± 0.2 (9.0–9.6)
RW***	4.4 ± 0.1 (4.1–4.7)	4.5	4.5/4.5	4.7 ± 0.1 (4.5–4.9)	4.7 ± 0.1 (4.5–4.9)	4.7 ± 0.1 (4.6–4.9)
IOW***	2.7 ± 0.1 (2.4–3.0)	2.6	2.7/3.0	2.9 ± 0.1 (2.7–3.1)	3.0 ± 0.1 (2.7–3.1)	2.8 ± 0.1 (2.7–3.0)
CC**	4.0 ± 0.1 (3.8–4.3)	4.1	4.2/4.0	3.9 ± 0.1 (3.6–4.1)	3.9 ± 0.1 (3.6–4.1)	4.0 ± 0.1 (3.8–4.1)
M^3M^3***	6.3 ± 0.2 (6.0–6.7)	6.3	6.7/6.4	6.1 ± 0.1 (5.9–6.3)	6.1 ± 0.1 (5.9–6.2)	6.1 ± 0.1 (6.0–6.3)
PL**	2.7 ± 0.1 (2.5–3.0)	2.9	2.8/2.8	2.6 ± 0.1 (2.4–2.9)	2.6 ± 0.1 (2.4–2.8)	2.7 ± 0.1 (2.5–2.9)
LTB	2.5 ± 0.1 (2.4–2.7)	2.6	2.7/2.6	2.6 ± 0.1 (2.5–2.7)	2.6 ± 0.1 (2.5–2.7)	2.5 ± 0.1 (2.5–2.7)
WCC***	2.4 ± 0.1 (2.3–2.6)	2.3	2.4/2.4	2.5 ± 0.1 (2.3–2.6)	2.4 ± 0.1 (2.3–2.6)	2.5 ± 0.1 (2.4–2.6)
DL	11.6 ± 0.2 (11.1–12.0)	11.7	11.6/11.5	11.7 ± 0.2 (11.3–12.1)	11.6 ± 0.2 (11.3–12.0)	11.7 ± 0.3 (11.5–12.1)
CM_3*	6.8 ± 0.1 (6.5–7.2)	6.9	7.0/7.1	6.9 ± 0.1 (6.6–7.1)	6.8 ± 0.1 (6.6–7.0)	7.0 ± 0.1 (6.7–7.1)
M_1M_3	4.4 ± 0.1 (4.2–4.7)	4.5	4.5/4.6	4.5 ± 0.1 (4.3–4.6)	4.4 ± 0.1 (4.3–4.5)	4.5 ± 0.1 (4.4–4.6)
CL**	2.1 ± 0.1 (1.8–2.3)	2.1	2.3/2.3	2.0 ± 0.1 (1.8–2.2)	2.0 ± 0.1 (1.8–2.1)	2.0 ± 0.1 (1.9–2.2)
CPH	2.8 ± 0.1 (2.6–3.2)	2.9	3.0/3.0	2.8 ± 0.1 (2.7–3.1)	2.8 ± 0.1 (2.7–3.0)	2.9 ± 0.1 (2.7–3.1)
CDH	2.0 ± 0.1 (1.8–2.2)	2.0	2.2/2.1	2.0 ± 0.1 (1.8–2.2)	2.1 ± 0.1 (1.9–2.2)	2.0 ± 0.2 (1.8–2.2)

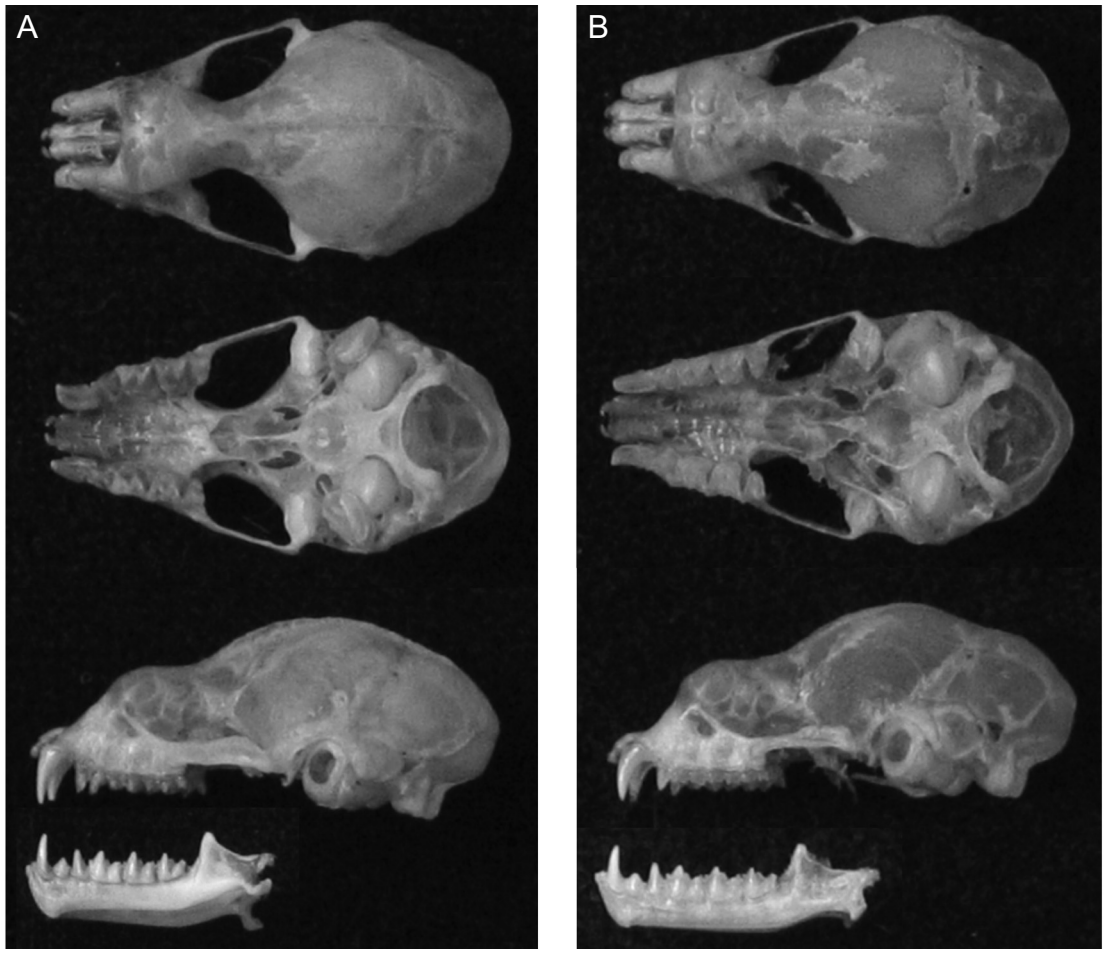

FIG. 6. Skull photographs taken at the same magnification: A — *H. kunzi* sp. nov. (=*H. bicolor*-142) and B — *H. bicolor* (=*H. bicolor*-131)

second function (Fig. 7A). However, the three individuals of *H. pomona* from peninsular Malaysia fell within *H. bicolor*-142, demonstrating their similarity in skull size and shape. In the leave-one-out analysis, all individuals were correctly classified in the initial analysis, except for six *H. bicolor*-142 that were misidentified as *H. pomona* and two *H. pomona* that were identified as *H. bicolor*-142, for an overall classification rate of 88.2%. There was lower accuracy in the cross-validation (83.9%), with 10 individuals of *H. bicolor*-142 misclassified as *H. pomona*, one *H. bicolor*-131 misidentified as

TABLE 4. Standardized canonical discriminant function coefficients and eigenvalues for a stepwise DFA comparing skull morphology of *H. bicolor* (=*H. bicolor*-131; including individuals from KWR and Borneo), *H. kunzi* (=*H. bicolor*-142), *H. cineraceus*-A, *H. cineraceus*-B, *H. halophyllus*, and *H. pomona*

Measurement	Function 1	Function 2	Function 3	Function 4	Function 5
GSL	-0.019	0.570	0.649	0.760	0.916
ZB	-0.032	-0.878	-0.104	-0.745	0.643
RW	-0.125	0.584	0.214	-0.822	-0.520
IOW	0.307	0.564	-0.563	0.139	0.249
M^3M^3	0.044	-0.581	-0.191	0.138	-0.342
DL	0.757	-0.029	0.129	-0.306	-0.562
M_1M_3	0.374	0.134	-0.705	0.556	-0.076
CDH	0.152	-0.028	0.579	0.377	-0.303
Eigenvalue	34.3	7.6	1.0	0.2	0.02
% of variance	79.5	17.6	2.4	0.5	0.00

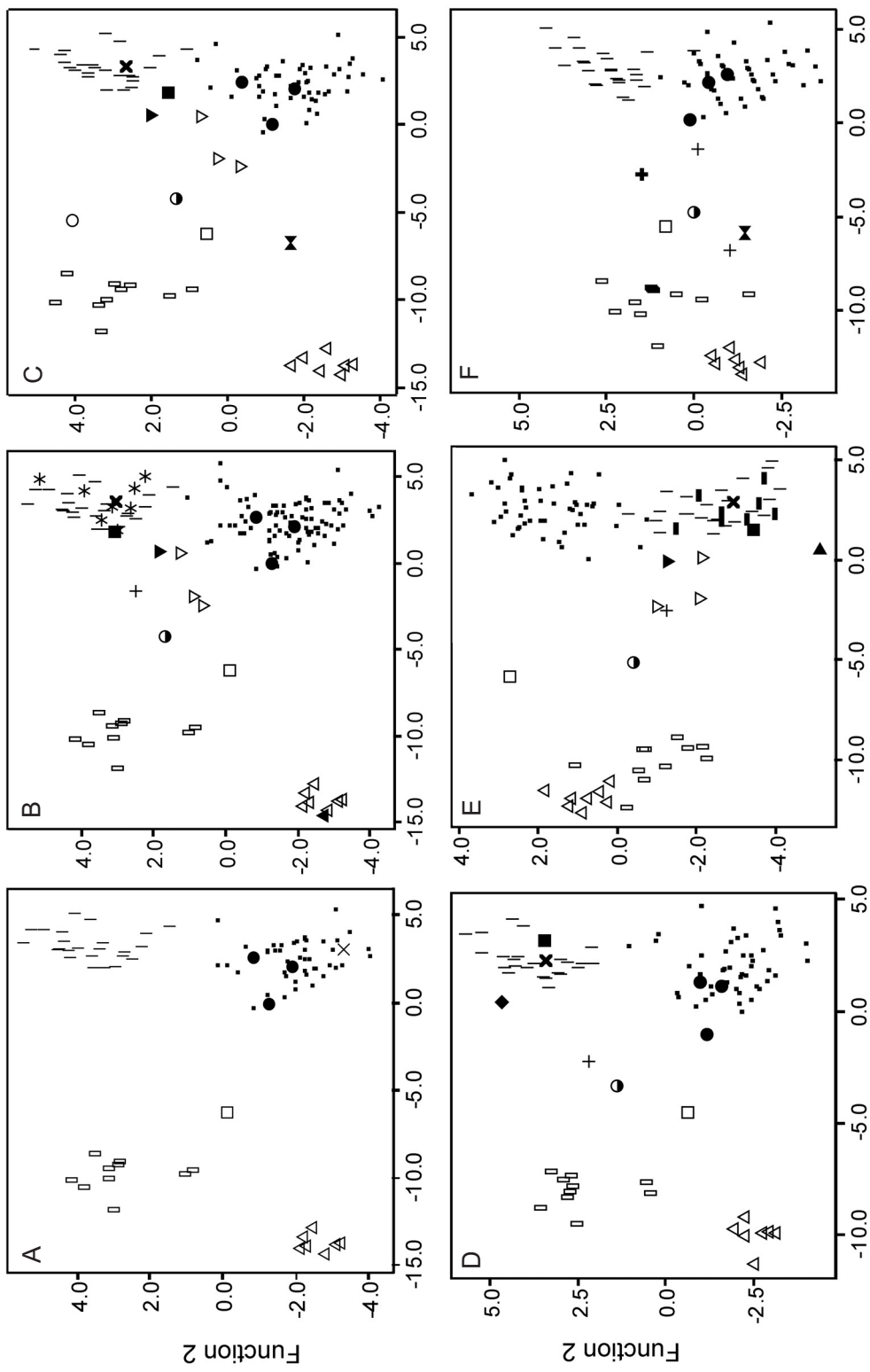

FIG. 7. Results of a stepwise DFA using 19 skull characters: A — The six different species from peninsular Malaysia were best separated with the first two functions: *H. bicolor* (|; = *H. bicolor*-131), *H. kunzi* sp. nov. (▪ = *H. bicolor*-142), *H. pomona* (●), *H. cineraceus*-A (▯), *H. cineraceus*-B (□), and *H. halophyllus* (△). Included is a paratype (TTU 108209) for *H. kunzi* sp. nov. (✕ = *H. bicolor*-142); B — The following specimens were entered into the resultant DFA to determine if they were conspecific with either *H. bicolor* or *H. kunzi*: *H bicolor* lectotype (✖), *H. pomona gentilis* type (◒), *H. bicolor major* type (■), type series of *H. javanicus* (✱), *H. bicolor erigens* paratypes (▽), *H. bicolor erigens* type (▼), *H. ater amboinensis* type (+), and *H. halophyllus* individual from Thailand (▲); C — One or two of the eight skull characters that best separated the six species from Malaysia were removed and the DFA was rerun to incorporated type specimens with incomplete skulls. GSL was removed to include the type specimen of *H. macrobullatus* (O) and the *H. pomona* type (✖); D — The type specimen for *H. bicolor atrox* (◆) was missing the dentary, so DL, M_1M_3, and CDH were removed from the analysis; E — IOW, RW, and M_1M_3 were removed to include *H. bicolor* from the Philippines (▶) and additional *H. bicolor* (= *H. bicolor*-131) from Sarawak (▬); F — The type specimen for *H. pomona sinensis* (✚) was more damaged than any of the other skulls, so a separate stepwise DFA was performed only including available skull characters. Four characters were retained: RW, M^3M^3, DL, and M_1M_3

H. bicolor-142, all three individuals of *H. pomona* identified as *H. bicolor*-142, and the single individual of *H. cineraceus*-B misclassified as *H. cineraceus*-A.

Next, the type specimens/series for which all eight informative skull characters could be measured were placed in the DFA to determine whether they fell within the ranges of either phonic type of *H. bicolor* (Fig. 7B). The lectotype of *H. bicolor* Temminck, 1834 (Naturalis, Leiden NL: RMNH 33654), the holotype of *H. bicolor major* Andersen, 1918 (Natural History Museum, London UK: BMNH 94.1.7.6), and the type series for *H. javanicus* Sody, 1937 (Naturalis, Leiden NL: Holotype RMNH 32178, type series includes RMNH 32164, 32694, 32712, 32713, 32714, 32715, and 32716; paratype RMNH 32167 was not included in the analyses as it had an incomplete skull; *H. javanicus* is currently synonymous with *H. bicolor*) all fell within *H. bicolor*-131. The type specimen for *H. pomona gentilis* (Natural History Museum, London UK: BMNH 93.11.15.2) was not associated with either phonic group of *H. bicolor* or *H. pomona* from Malaysia. The paratypes (Museum of Comparative Zoology, Harvard USA: MCZ 35195, 35196, and 35198) and holotype (MCZ 35197) of *H. bicolor erigens* formed a loose cluster separated from both phonic types of *H. bicolor*. The *H. ater amboinensis* syntype (Naturalis, Leiden NL: RMNH 33657) for which all characters were available fell outside all other groups in the analysis; the second syntype had an incomplete skull (Naturalis, Leiden NL: RMNH 33657).

The remaining type specimens had incomplete skulls that did not have all eight skull characters retained in the stepwise DFA. For these individuals, we removed one or more variables and re-ran the DFA with the remaining characters. GSL could not be measured for the *H. macrobullatus* (American Museum of Natural History, New York USA: AMNH 102367) and *H. pomona* (Natural History Museum, London UK: BMNH 18.8.3.4) type specimens. In a DFA without this character, there was a 91.4% classification rate, and 88.2% accuracy in the cross-validation. The separation among species with the first two functions was similar to the original DFA (Fig. 7C). Neither *H. macrobullatus* nor the type specimen for *H. pomona* overlapped with either phonic type of *H. bicolor*, or with *H. pomona*.

The type specimen for *H. bicolor atrox* (Natural History Museum, London UK: BMNH 1.3.9.4) was missing its dentary. When we removed DL, M_1M_3, and CDH from the DFA, 91.4% and 87.1% of individuals were classified correctly in the classification and cross-validation, respectively. As in the previous analyses, five of the six species were well differentiated using the first two functions, with *H. pomona* falling within *H. bicolor*-142 (Fig. 7D). *Hipposideros bicolor atrox* fell within the upper limits of the *H. bicolor*-131 group.

The type series of *H. b. erigens* (Museum of Comparative Zoology, Harvard USA: MCZ 35195, 35196, 35197, and 35198), a subspecies described from the Philippines, was used to examine the status of the individual identified as *H. bicolor* from the Philippines (Field Museum, Chicago USA: FMNH 180193). Individuals of *H. bicolor*-131 from Sarawak (Fig. 1: site 15) were also included in the analysis. The three skull characters (IOW, RW, M_1M_3) that were missing were removed from the DFA. In the leave-one-out classification of the six species from peninsular Malaysia, 89.3% and 87.4% of individuals were correctly identified in the original and cross-validation, respectively. The Philippine individual identified as *H. bicolor* based on external morphology was not similar in skull morphology to *H. b. erigens* or any other group in the analysis (Fig. 7E). As expected, the *H. bicolor*-131 from Sarawak fell within the group of other *H. bicolor*-131 from KWR and Borneo.

We asked whether the type specimen of *H. pomona sinensis* (Natural History Museum, London UK: BMNH 92.2.1.3) fell within any of the six species from peninsular Malaysia. The type specimens for *H. p. gentilis* and *H. pomona* were included in the analysis as references. The 13 characters that could be measured for the *H. p. sinensis* type were entered into a stepwise DFA; four characters (RW, M^3M^3, DL, and M_1M_3) and four functions were retained in the analysis. The leave-one-out classification had lower accuracy than any of the previous analyses, with 75.8% and 71.6% of individuals identified correctly in the original and cross-validation, respectively. None of the type specimens, including *H. p. sinensis*, fell within the ranges of *H. bicolor*-131, *H. bicolor*-142, or *H. pomona* (Fig. 7F). Both the damaged (Naturalis, Leiden NL: RMNH 33658) and undamaged skulls (Naturalis, Leiden NL: RMNH 33657) for the *H. ater amboinensis* syntypes were included in this analysis because these individuals were a part of the *H. bicolor* paralectotype series prior to being synonymized with *H. ater*. Interestingly, the two *H. ater amboinensis* skulls did not cluster together (Fig. 7F).

Finally, we evaluated the relationship between the subspecies named in Kitchener *et al*. (1996) and

the species examined in the current study. However, only nine skull characters overlapped between the two studies and the analysis was performed using the mean values (Kitchener *et al*., 1996: Table 2). Thus, the comparison between the studies is cursory and taxonomic changes will require more rigorous analyses. Eight skull characters (GSL, M^1M^3, MW, ZW, IOW M^3M^3, LTB, and DL) and five functions were retained in the stepwise discriminant function analysis, with separation along the first two functions very similar to the previous analyses (Fig. 8). Two patterns were evident in comparing the taxa in the current study to those studied by Kitchener *et al*. (1996). First, while the type specimen of *H. b. atrox* fell within *H. bicolor*-131 in the present study (Fig. 7D), the mean values of the skull variables for the three individuals Kitchener *et al*. (1996) identified as *H. b. atrox* fell well within *H. bicolor*-142 (Fig. 8). This suggests that Kitchener *et al*. (1996) used individuals of *H. bicolor*-142 in their study. Second, the subspecies described by Kitchener *et al*. (1996) all fell between *H. bicolor*-131 and *H. bicolor*-142, with *H. b. hilli*, *H. b. selatan*, and the individuals from Sumbawa and Sumba falling along the edge of *H. bicolor*-131, and *H. b. tanimbarensis* along the edge of *H. bicolor*-142 (Fig. 8).

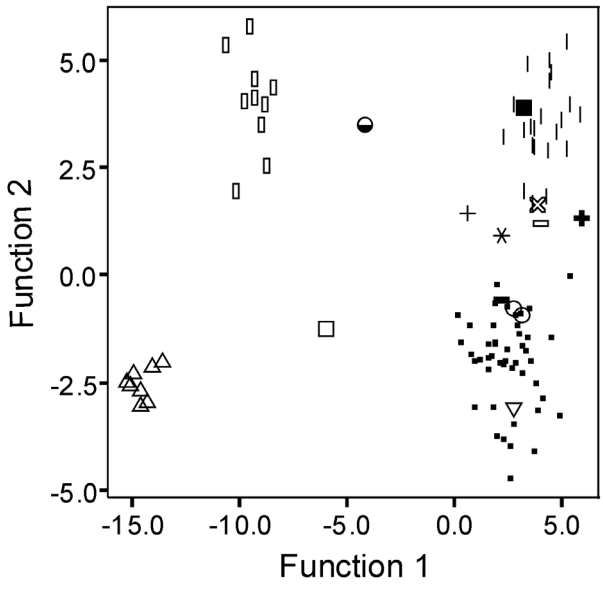

FIG. 8. Results of stepwise discriminant function analysis including data from this study and Kitchener *et al*. (1996). Species measured in the current study included, *H. bicolor* (1 = *H. bicolor*-131; including individuals from KWR and Borneo), *H. kunzi* sp. nov. (■ = *H. bicolor*-142), *H. pomona* (○), *H. cineraceus*-A (▯), *H. cineraceus*-B (□), *H. halophyllus* (△), and the type specimens for *H. pomona gentilis* (◒) and *H. b. major* (■). Measurements were taken from Kitchener *et al*. (1996) for the following: *H. bicolor atrox* from peninsular Malaysia (▽), *H. b. bicolor* from Java (⨳), *H. b. tanimbarensis* (━), *H. b. hilli* (+), *H. b. selatan* (∗), *H. bicolor* from Sumbawa (✚), and *H. bicolor* from Sumba (▭)

Karyotype Analyses

Karyotypes were compared between female individuals of *H. bicolor*-131 and *H. bicolor*-142. Karyotype spreads were produced for two individuals of *H. bicolor*-131: TTU108176 (TK152013) and TK152015 (Voucher specimen deposited in Universiti Malaysia Sarawak) and a single individual of *H. bicolor*-142 TTU108209 (TK152051). Based on the combination of fundamental and diploid number, *H. bicolor*-131 and *H. bicolor*-142 had karyotypes that were indistinguishable from each other. The diploid number (2N) was 32, and the fundamental number (FN) was 58. There were 11 metacentric/submetacentric pairs, two subtelocentric pairs, two indistinguishable pairs of either subtelocentric or submetacentric, one acrocentric pair, and one pair of X-chromosomes.

Habitat, Distribution and Relative Abundance

A total of 1,745 individuals identified as belonging to the *H. bicolor* complex were captured in KWR and 25 caves and cave-like structures in peninsular Malaysia and southern Thailand during this study. Of these, we were able to classify 1,403 adults to species based on morphology, echolocation call frequency and/or mitochondrial haplotype; 201 juvenile individuals were eliminated from this analysis and 141 adults could not be accurately identified based on morphology alone. Of the correctly classified individuals, 1,223 were *H. bicolor*-142 and 180 were *H. bicolor*-131. In the karst regions sampled in this study, *H. bicolor*-142 was a relatively widespread and common bat, with individuals being captured in caves at all sampling localities in peninsular Malaysia and Thailand (Fig. 1). Individuals of *H. bicolor*-142 also were captured at the forest sites sampled in this study: Krau Wildlife Reserve, a small forest preserve in Taiping, and Kuala Atok.

Hipposideros bicolor-142 colonies were found in caves, mines, and an underground overflow system for an impounded reservoir. Colonies varied in size from a few individuals to several hundred. Although *H. bicolor*-142 was captured exiting a few dry caves, individuals were mostly found roosting in caves with standing or flowing water or high humidity. It is unknown whether *H. bicolor*-142 roosts

preferentially in high humidity caves, or if most available caves had some form of water in them. *Hipposideros bicolor*-142 was the only species roosting in Batu Belah cave in KWR; all other caves were occupied by several different species in addition to *H. bicolor*-142.

In contrast, to *H. bicolor*-142, *H. bicolor*-131 was almost exclusively captured in forested areas in peninsular Malaysia, including Taiping, Kuala Atok, and Krau Wildlife Reserve. Despite extensive sampling at caves throughout peninsular Malaysia, *H. bicolor*-131 was only captured at two cave-like structures, both of which were adjacent to KWR: a shallow hill-side cave known locally as Samad Cave, and a rocky outcrop near Jenderak Selatan.

Discussion

The systematics of the *bicolor* species group has been contentious for a century (e.g., Andersen, 1918; Hill, 1963; Douangboubpha *et al*., 2010). In this study, we resolve the taxonomy of the namesake of this group, *H. bicolor*. Since the first description of the Malaysian *H. bicolor* phonic types (Kingston *et al*., 2001), morphological, echolocation call frequency and genetic data have supported the recognition of *H. bicolor*-131 and *H. bicolor*-142 as distinct species (Kingston *et al*., 2001; Douangboubpha *et al*., 2010; Murray *et al*., 2012). Here, with large sample sizes for all three types of data, we find strong support for species status for *H. bicolor*-131 and *H. bicolor*-142. Comprehensive analysis of all available type material indicates that *H. bicolor*-131 should retain the species name, as proposed by Douangboubpha *et al*. (2010). In contrast, our analyses support that *H. bicolor*-142 is distinct from all previously named species and subspecies, including *H. bicolor atrox.* Below, we highlight the major genetic, morphological, and ecological differences between *H. bicolor*-142 and *H. bicolor*-131. We review the taxonomy of *H. bicolor* in light of our results, and close with the species description and new species name for *H. bicolor*-142.

Intraspecific Genetic Structure

Hipposideros bicolor-131 was comprised of three mitochondrial haplotype groups: Borneo, and two peninsular Malaysian groups: Taiping and KWR (Figs. 2 and 3). Haplotypes from Borneo were relatively undifferentiated (0.2–2.4% sequence divergence — Table 1) across geographic distances ranging from approximately 300 to 1,000 km (Fig. 1), a pattern consistent with ongoing high gene flow among populations, or with an evolutionarily recent range expansion. While discriminating between these scenarios awaits population genetic analyses with more comprehensive sampling and additional molecular markers, this bat's small size and strong association with forest suggests that high ongoing gene flow is less likely. Dry land connections between Borneo and mainland southeast Asia during Pleistocene glacial maxima provided opportunities for range expansion in multiple species, including bats (Voris, 2000; Bird *et al*., 2005).

Despite extensive sampling throughout peninsular Malaysia, *H. bicolor*-131 was only captured at three sites: Taiping in the northern state of Perak, Kuala Atok and KWR, the latter two sites being adjacent in the central state of Pahang (Fig. 1). In contrast to the Borneo clade, haplotypes from the Taiping and KWR groups differed by 4.7–5.1%, over a maximum distance of approximately 200 km. While this deep divergence suggests long-term isolation between mitochondrial lineages, there is no evidence for historic barriers to gene flow between northern and central peninsular Malaysia. Moreover, the occurrence of both Taiping and KWR haplotypes at Kuala Atok indicates that the haplotype groups are not geographically isolated. It will be of great interest to determine whether there is nuclear gene flow between these mitochondrial lineages.

In contrast to *H. bicolor*-131, *H. bicolor*-142 was characterized by low levels of genetic differentiation among three mitochondrial haplotype groups: Malay, Thai, and Perlis (Figs. 2 and 4, and Table 1). There was little genetic differentiation within the Malay and Thai groups; haplotypes of the Malay group were recovered at all sites sampled in peninsular Malaysia and there was no evidence of geographic structure. There was more structure within the Perlis group, with two well-supported haplotype clades with 2% observed sequence divergence between them (Figs. 2, 4, and Table 1) from sites less than 15 km apart. Interestingly, this division corresponds to the two main ranges of limestone hills in Perlis that run north to south: the Setul formation forms a long range that runs along the west coast and north into Thailand, while the Chuping formation is made up of individual hills in central Perlis (Price, 2001). This pattern of differentiation could be explained by historic separation between the two haplotype groups and/or limited dispersal of females between the two formations. A more extensive population genetic study that includes nuclear and Y-linked markers will be needed to infer the historical

demography of the Perlis haplotype groups, and the extent of gene flow between the Setul and Chuping formations.

Interspecific Differences in Genetic Structure and Ecology

The overall patterns of higher between-population differentiation and within-population variation in *H. bicolor*-131 relative to *H. bicolor*-142 could be explained by stochastic differences in demographic history and geographic origin. However, ecological factors such as dispersal ability, colony size, social structure, roost type and habitat association can also influence genetic structure in bats (e.g., Rossiter *et al*., 2012; Sagot *et al*., 2016).

In peninsular Malaysia, *H. bicolor*-131 was captured almost exclusively in forests. This result is consistent with previous surveys of bat diversity on the Malay peninsula that documented a *H. bicolor*-131-like morph of *H. bicolor* at lowland forest sites (Francis, 1990, 1995; Lim *et al*., 2014), but contrasts with survey results in Thailand, where the species was captured both in lowland forest and human-modified habitats (secondary forest, rubber plantations, cultivated areas, human settlements; Douangboubpha *et al*., 2010). Despite an extensive survey of caves at five different karst regions in peninsular Malaysia, we captured *H. bicolor*-131 at only two cave sites, a small cave just outside of KWR and an area with rock crevices inside KWR. In contrast, *H. bicolor*-142 in Malaysia was found in habitats ranging from relatively pristine lowland forest (e.g., KWR) to open, agricultural areas (e.g., the Chuping formation in central Perlis), and was captured in the majority of caves that were found to house insectivorous bats. Similarly, Douangboupha *et al*. (2010) collected this species in or near limestone caves surrounded by diverse habitats, and it appeared tolerant of landscape disturbance. These patterns indicate that, in peninsular Malaysia, *H. bicolor*-131 is forest-dependent, whereas *H. bicolor*-142 is more tolerant of disturbance and exploits a wider range of habitats including caves.

Interspecific Differences in Morphology

Although *H. bicolor*-131 and *H. bicolor*-142 were often difficult to differentiate in the field and in museum collections, there were some quantifiable differences in morphology. In general, *H. bicolor*-131 had a lighter colored nose, and the posterior noseleaf tended to be taller than that of *H. bicolor*-142 (Fig. 9), but these traits were subjective and not always consistent. Overlap existed in the measures of external morphology, but overall *H. bicolor*-131 was significantly larger (Table 2). Lengths of tibia and forearm were the most useful external measures in differentiating between *H. bicolor*-131 and *H. bicolor*-142.

In general, *H. bicolor*-131 had larger wings with more rounded wings and wingtips compared to *H. bicolor*-142. These basic differences in wing morphology were also reported by Kingston *et al*. (2001). Based on wing morphology, harp-trapping surveys (e.g., Kingston *et al*., 2000), and an echolocation survey of both forests and open areas (Douangboupha *et al*., 2010; T. Wood, personal communication), both *H. bicolor* phonic types are thought to forage in forested areas. Lower wing loading, lower aspect ratio, and more rounded wing tips all indicate that *H. bicolor*-131 is potentially more maneuverable than *H. bicolor*-142 (i.e., Norberg and Rayner, 1987), and therefore better-adapted to feeding in cluttered microhabitat. Tests of flight performance (ability to navigate an obstacle course) of 15 understory insectivorous bats from KWR confirmed that both species are highly maneuverable and able to readily fly through obstacles (string sets) less than 10 cm apart. However, no difference in performance between the phonic types was observed (Juliana, 2015).

Although overall skull appearance is very similar between the two phonic types of *H. bicolor* (Fig. 6), they differed significantly in both skull shape and size (Table 3). Compared to *H. bicolor*-142, the skull of *H. bicolor*-131 was significantly longer, narrower across the zygomatic arches, wider across the rostrum and at the constriction behind the orbits, had a narrower, shorter palate, a taller rostrum, a shorter braincase, and shorter canines in both the upper and lower jaws. These differences are congruent with those described by Douangboubpha *et al*. (2010).

Differences in Call Frequency

In the first description of the two *H. bicolor* phonic types at KWR, Kingston *et al*. (2001) found a difference in echolocation call frequency much larger than expected based on difference in body size, and a 5 kHz silent band between the upper frequency range of *H. bicolor*-131 and the lower frequency range of *H. bicolor*-142. With a larger number of calls, sampled from multiple localities in peninsular Malaysia, our results strongly support the call frequency difference between *H. bicolor*-131

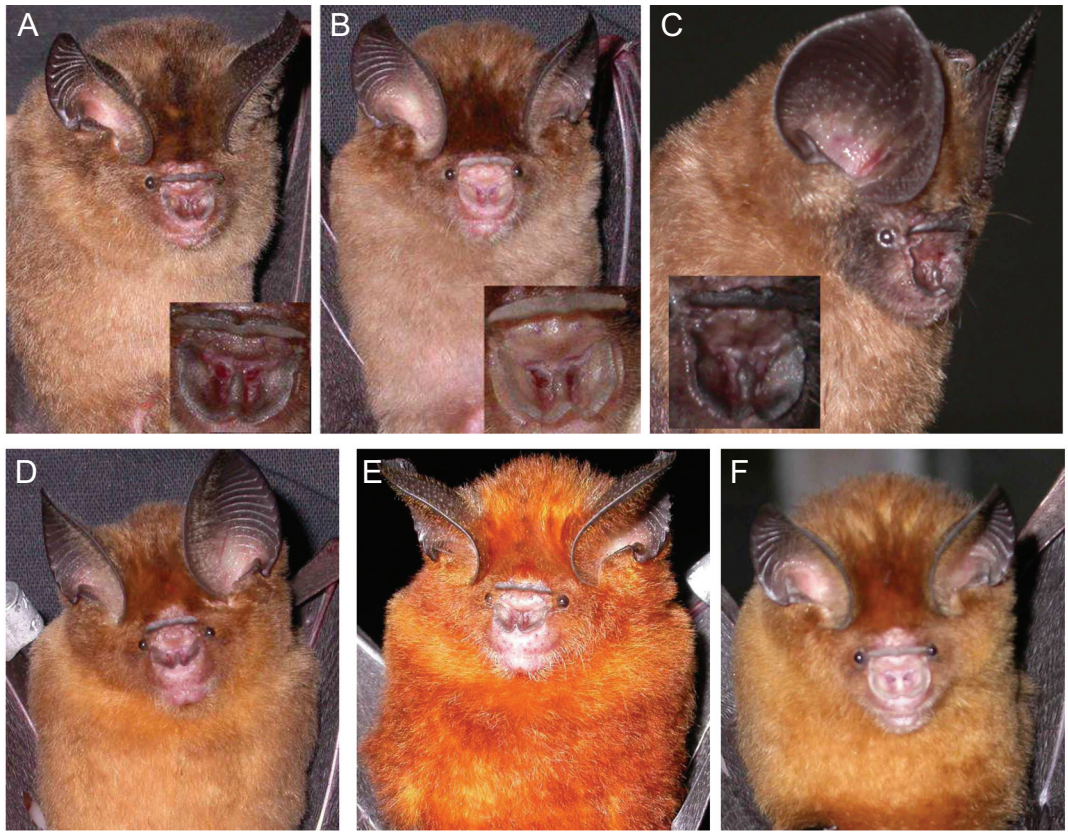

FIG. 9. Photographs of *H. kunzi* sp. nov. (=*H. bicolor*-142; A, D, and E) and *H. bicolor* (=*H. bicolor*-131; B and F), demonstrating overall similarity in appearance, variations in coat color, and differences in nose coloration (insets). *Hipposideros cineraceus*-B (C) is closely related to *H. kunzi* genetically, but is easily distinguished based on nose morphology and body size. Photographs are not to scale

and *H. bicolor*-142, and indicate that these two phonic types co-occur at multiple sites. However, we found a wider range in call frequency for both *H. bicolor*-131 and *H. bicolor*-142 than that documented by Kingston *et al*. (2001), which resulted in a narrow band of overlap centered at ca. 135 kHz.

Taxonomy

There are three species in peninsular Malaysia (this study) and Thailand (Douangboubpha *et al*., 2010) that are very similar in appearance and size, but genetically distinct: *H. pomona*, *H. bicolor*-142, and *H. bicolor*-131 (Fig. 2). The taxonomic histories of *H. bicolor* (originally described from Java) and *H. pomona* (described from Southern India) are intertwined. Hill (1963) synonymized *H. pomona* and *H. gentilis* (including *atrox*, *gentilis*, *major*, and *sinensis*), and placed them as subspecies of *H. bicolor*. Later, Hill *et al*. (1986) recognized *H. pomona* as a separate species with *gentilis* (Northern India and Myanmar) and *sinensis* (China and Thailand) as subspecies, and retained *atrox* (peninsular Malaysia), *major* (Nias and Enggano Islands, off the west coast of Sumatra), and *erigens* (Philippines) as subspecies of *H. bicolor*. Our cranial analyses support the separation of *H. pomona pomona*, *H. p. gentilis*, and *H. p. sinensis* from both *H. bicolor* phonic types (Fig. 7). However, the individuals identified as *H. pomona* from peninsular Malaysia were also clearly distinct from the type specimens of *H. pomona*, *H. p. gentilis*, and *H. p. sinensis*. Skull morphology of *H. pomona* from Malaysia overlapped with *H. bicolor*-142 (Fig. 7A), a result also found in Thailand (Douangboubpha *et al*., 2010). However, genetic data placed *H. pomona* individuals from Malaysia in the same clade as other individuals identified as *H. pomona* from Myanmar, southern China, and Laos (Fig. 2; Murray *et al*., 2012). The distribution of *H. pomona* as it is currently defined is disjunct, with records from southern India, Nepal, Myanmar, Thailand, Laos, Vietnam, peninsular Malaysia, and southern China (Bates and Harrison, 1997). It is likely that *H. pomona* from peninsular Malaysia represents a taxon distinct from

H. pomona from S. India, a conclusion also proposed by Douangboubpha *et al*. (2010).

The *H. bicolor* type series, as established by Tate (1941), contained four paralectotypes from Ambon (Naturalis, Leiden NL: RMNH 33655, 33656, 33657, 33658) and three individuals from Java (Lectotype RMNH 33654 and paralectotypes RMNH 33652 and 33653). The two skulls available from the Ambon individuals (RMNH 33657 and 33658) were morphologically distinct from the *H. bicolor bicolor* lectotype (Fig. 7B), supporting previous interpretations of the *H. bicolor* type series as comprising two distinct species: *H. ater amboinensis* from Ambon and *H. b. bicolor* from Java (Peters, 1871; Tate, 1941; Hill, 1963; Bergmans and Van Bree, 1986). The three individuals from Java in the type series included an adult female, the lectotype (RMNH 33654), and two subadults (RMNH 33652 and 33653), which did not have their skulls extracted (C. Smeenk, personal communication). Our measurement of forearm length (FA = 44.5 mm) for the *H. b. bicolor* lectotype is similar to that of an adult *H. bicolor* from Java (FA = 43 mm) given by Temminck (1835). Tate (1941), however, reported the forearm of the lectotype as much longer (47 mm), which is likely why Hill (1963) thought Tate had transferred the name *H. bicolor* to a specimen of a larger *bicolor*-like species, namely *H. pomona* or *H. gentilis*. The entire type series was mounted standing upright with wings spread, making it very difficult to accurately measure the specimens. Because of the poor condition of the skins and the similarity in external morphology between the two species of *H. bicolor* under study, we chose to base taxonomic decisions on the skull morphology of the lectotype.

Based on skull morphology, the *H. b. bicolor* lectotype fell within the range of *H. bicolor*-131 (Fig. 7B). We therefore agree with Douangboubpha *et al*. (2010) that *H. bicolor*-131 should retain the name *H. bicolor*. Consequently, *H. bicolor*-142 could represent one of the remaining six subspecies of *H. bicolor* (*atrox*, *erigens*, *hilli*, *major*, *selatan*, and *tanimbarensis*) or its one synonym (*H. javanicus*; Simmons, 2005). Several studies have suggested that *H. javanicus* is conspecific with *H. b. bicolor* (Tate, 1941; Hill, 1963; Hill *et al*., 1986), which is consistent with our results: the type series of *H. javanicus* fell within the same grouping as *H. bicolor*-131 and the lectotype of *H. bicolor* (Fig. 7B). The type specimen of *H. bicolor major* also fell within *H. bicolor*-131, while the type specimen of *H. b. atrox* fell along the periphery of *H. bicolor*-131 (Fig. 7B and 7D), suggesting that both should remain as subspecies of *H. bicolor*. Thus, we find no support for the suggestion that *H. bicolor*-142 should be referred to *atrox*, the next available name (Douangboubpha *et al*., 2010). Although the holotype of *atrox* evaluated by Douangboubpha *et al*. (2010) was larger than *H. bicolor*-142 from Thailand and an outlier in their analysis of cranial characters (Douangboubpha *et al*., 2010: figure 8), they argued that the morphology of *H. bicolor*-142 was consistent with that of *H. b. atrox* in Hill (1963) and Zubaid and Davison (1987). However, the results of our survey of 12 sites in peninsular Malaysia suggest that, in peninsular Malaysia, *H. bicolor*-142 is generally more common than *H. bicolor*-131. Therefore, we think it likely that at least some of the specimens assigned to *H. b. atrox* by Hill (1963), Hill *et al*. (1986), and Zubaid and Davison (1987) represent *H. bicolor*-142. This confusion would explain the overlap between the *H. bicolor*-142 studied by Douangboubpha *et al*. (2010) and the '*H. b. atrox*' in the earlier studies. It is interesting to note that when Andersen (1918) described *H. gentilis atrox* from peninsular Malaysia, he likely measured specimens of both *H. bicolor*-131 and *H. bicolor*-142: the published forearm measurements for this subspecies have the largest variation within *H. gentilis*, with a range that overlaps with both *H. bicolor* phonic types.

Our data indicate that the remaining subspecies of *H. bicolor* (*erigens*, *hilli*, *selatan*, and *tanimbarensis*) are not conspecific with *H. bicolor*-142, based on either skull morphology (Figs. 7 and 8) or geographic location. Lawrence (1939) distinguished *H. erigens* from *H. ater antricola* in the Philippines, but other authors found it to be conspecific with *H. bicolor* (Hill, 1963; Hill *et al*., 1986). In the current study, the type series of *H. b. erigens* were distinct in skull morphology from both phonic types of *H. bicolor*, and from the individual of *H. bicolor* from the Philippines (Fig. 7E). The individual from the Philippines that was identified in the field as *H. bicolor* (Field Museum, Chicago USA: FMNH 180193) and closely resembled *H. bicolor*-142 in external morphology (J. Sedlock, personal communication) was genetically distinct from all other *H. bicolor* (Fig. 2; see also Murray *et al*., 2012 and Esselstyn *et al*., 2012). These results indicate that *H. b. erigens* may warrant reinstatement to specific status and that a re-examination of *H. bicolor* and its allies in the Philippines is needed.

Kitchener *et al*. (1996) described three new subspecies of *H. bicolor* that ranged across the lesser Sunda islands: *H. b. tanimbarensis* from Selaru and

Sumba, *H. b. hilli* from Timor, and *H. b. selatan* from Roti and Savu. These subspecies were defined as morphologically distinct from *H. bicolor atrox* from peninsular Malaysia, and more similar to *H. b. bicolor* from Java (Kitchener *et al*., 1996). Based on external and skull morphology we found that the specimens of *H. b. atrox* used in Kitchener's study were in fact *H. bicolor*-142, whereas the Lesser Sunda subspecies were intermediate to *H. bicolor*-142 and *H. bicolor*-131 (Fig. 8). Therefore, morphological data indicate that *H. bicolor*-142 is not conspecific with the subspecies described by Kitchener *et al*. (1996).

To our knowledge, *H. macrobullatus* and *H. fulvus* (including the subspecies *pallidus* and synonyms *murinus*, *fulgens*, *aurita*, and *atra*) are the only other species or previously named forms that are morphologically similar to *H. bicolor*-142. We found that *H. macrobullatus* is morphologically distinct from all *H. bicolor* forms in this study (Fig. 7C). *Hipposideros fulvus* was not included in this study because it is currently restricted to the Indian subcontinent (Bates and Harrison, 1997), and there is approximately 12% observed sequence divergence in the ND2 gene between this species and *H. bicolor*-142 (Murray *et al*., 2012). Because the skull morphology of *H. bicolor*-142 is distinct from the synonyms of *H. bicolor* (*atrox*, *erigens*, *javanicus*, *major*, *hilli*, *tanibarensis*, and *selatan*), closely allied species *H. pomona* (*sinensis* and *gentilis*), and *H. macrobullatus*, we recommend *H. bicolor*-142 be recognized as a new species and given a new name, as described in the following section.

Systematic Description

Hipposideros kunzi sp. nov. Murray, Khan, Kingston, Akbar, and Campbell
Kunz's bicolored leaf-nosed bat

Hipposideros bicolor (Temminck, 1834), part.
Hipposideros atrox (Andersen, 1918), part.
Hipposideros bicolor atrox (Kitchener *et al*., 1996), part.
Hipposideros bicolor-142 (Kingston *et al*., 2001)
Hipposideros atrox (Douangboupha *et al*., 2010)

Etymology

The species is named after Thomas H. Kunz in recognition of his many contributions to the ecology and conservation of bats, and his dedication to the promotion of bat research in Malaysia.

Holotype

Texas Tech University TTU 108222 (tissue and karyotype TK 152065; field number VJS 155), adult ♂, body in alcohol, skull extracted, collected and photographed by Robert J. Baker on 6 August 2006 during TTU-UNIMAS Sowell Expedition (Khan *et al*., 2008). Although the echolocation calls were not recorded for the holotype and the paratypes described here, all of the type specimens had mtDNA haplotypes consistent with the 142 kHz phonic group. This was further supported through comparisons of the noseleaf morphology with that of individuals for which the echolocation call frequency was known.

Measurements (in mm) — forearm length: 43.31; fifth, fourth, and third metacarpals lengths, respectively: 32.20, 33.87, 32.88. Length of first and second phalanges of third digits, respectively: 17.47, 16.46; tail length: 25.0; hind-foot length: 7.0; tibia length: 19.70; ear height: 17; body mass: 6.5 g; anterior noseleaf width: 4.66. Skull measurements are provided in Table 3.

Type locality

Bukit Rengit, Krau Wildlife Reserve, Pahang, Peninsular Malaysia (WGS84 03°35'45.6"N, 102°10' 59.0"E — approximate elevation 72 m). The specimen was collected using a harp trap set across a trail near the Institute of Biological Diversity at Bukit Rengit.

Paratypes

Texas Tech University TTU 108417 (tissue and karyotype number TK 152001), adult ♂ (4 August 2006), dry skin and skull with slight crack in brain case; TTU 108209 (tissue number TK 152051), adult ♀ (6 August 2006), dry skin (housed at the Universiti Malaysia Sarawak, but missing) and skull (housed at the Texas Tech University). Both TTU 108417 and TTU 108209 were captured in Krau Wildlife Reserve (03°35'45.6"N, 102°10'59.0"E — elevation 72 m). Specimen TK 152992, adult ♀ (17 May 2008), dry skin and skull in Department of Wildlife and National Park (DWNP), Malaysia; specimen TK 153519, adult ♀ (20 May 2008), alcohol preserved specimen at Universiti Malaysia Sarawak. Both TK152992 and 153519 were collected by FAAK during DWNP biodiversity inventory at Kuala Atok, Pahang, peninsular Malaysia (04°16.281'N 102°22.316'E — approximate elevation 85 m).

Taxonomic notes

All specimens previously referred to *H. atrox* (Douangboubpha *et al*., 2010) and *H. bicolor*-142 are here referred to *H. kunzi* sp. nov. Based on length

of forearm, Hill (1963) likely included both *H. bicolor* and *H. kunzi* as *H. bicolor atrox*, although the majority of these individuals are probably *H. kunzi* based on length of forearm (p. 29, Fig. 4). We cautiously assign the individuals of *H. bicolor atrox* from both Hill *et al*. (1986) and Zubaid and Davison (1987) to *H. kunzi*. It is unclear where the bats were collected, but it is suggested they were captured in Northern peninsular Malaysia, which would suggest that they are indeed *H. kunzi*. In his description of the new species *Hipposideros gentilis*, Andersen (1918) described the new subspecies *H. g. atrox* as having a wide range of forearm lengths that span both *H. bicolor* and *H. kunzi*: 42–46.2 mm (Andersen, 1918: 380). Thus he likely measured both individuals of *H. bicolor* and *H. kunzi* for the subspecies description.

Description

This is a small to medium-sized hipposiderid bat in the *H. bicolor* group with a forearm length ranging from 38.8 to 45.6 mm (mean = 42.9 mm ± 0.9), tibia length of 17.1 to 20.6 mm (mean = 18.8 mm ± 0.5), and mass varying from 6.0 to 12.0 g (mean = 8.5 g ± 0.9 — Table 2). The dorsal pelage varies from medium or dark brown to bright orange, but is always bicolored with a white base. The ventral pelage ranges from buff or golden, to bright orange (Fig. 9). The wing and tail membranes are dark brown, as are the ears. The ears are large (mean = 17.6 mm ± 0.6) and rounded with a bluntly pointed tip. The noseleaf lacks supplementary lateral leaflets and has an internarial septum that is generally triangular in shape (wider at the base — Fig. 9). The posterior and anterior portions of the nose are dark brown-grey in color, while the central part of the noseleaf is more flesh colored. The tail is long (mean = 28.7 mm ± 1.8), extending the full length of the uropatagium. The fifth metacarpal is about 74% of forearm length and the first phalanx of the third digit is about 53% of third metacarpal. Echolocation call frequency of the CF component ranges from 133.2 to 147.5 kHz, with a mean call frequency of 143.1 ± 2.0 kHz (Fig. 5 and Table 2).

Hipposideros kunzi has a small and elongate skull with the greatest length of skull (GSL) ranging from 17.69 to 19.13 mm (mean = 18.31 ± 0.33 mm). The skull is slightly wider across the zygomata (mean = 9.2 ± 0.2 mm) compared to across the mastoids (mean = 9.2 ± 0.2 mm — Table 3). The distal process of the jugal bone is low and not well defined (Fig. 6). The rostrum is well developed with six nasal inflations. The sagittal crest is well developed and is taller more anteriorly. The constriction behind the orbits is well defined and narrower than the rostrum. The upper toothrow is shorter (CM^3 mean = 6.3 ± 0.1 mm) than the lower (CM_3 mean = 6.8 ± 0.1 mm). The upper incisor is small and both the upper and lower canines are of moderate size. The upper premolar (P^2) is minute and extruded from the toothrow, while the lower premolar (P_2) is about half the height of the second premolar (P_4). The species is sexually dimorphic with respect to magnitude of certain skull measurements: despite being smaller than females, males have longer and taller skulls and longer canines.

Comparisons with similar species

Hipposideros kunzi is one of several *Hipposideros* species described from the Indo-Malayan region, which superficially resemble *H. bicolor* and lack supplementary leaflets adjacent to the noseleaf. In peninsular Malaysia and southern Thailand, *H. kunzi* most closely resembles, and is easily confused with, both *H. bicolor* and *H. pomona*. Compared to *H. bicolor*, *H. kunzi* has a higher echolocation call frequency (Table 2), is generally smaller in body size (Table 2), and has a shorter but wider skull (Table 3 and Fig. 9). In addition, *H. kunzi* has a narrower anterior noseleaf (Holotype: 4.66 mm) that is slightly curved upwards compared to *H. bicolor*, which has a wider anterior noseleaf (4.94−5.46 mm, n = 5) that is flattened and square in appearance (Kingston *et al*., 2006), lighter in color, and has rudimentary supplementary lateral leaflets (Fig. 9). The noseleaf characters, however, are only useful if both species are available for comparison in the field.

Based on appearance (Murray *et al*., 2012: figure S1), echolocation call frequency (*H. pomona*: 136.4 –139.4 kHz, n = 3), overall size (*H. pomona* length of forearm: 42.7–44.8 mm, n = 3), and skull size and shape (Fig. 7), it is very difficult to distinguish *H. kunzi* from *H. pomona*. The main morphological difference between these species is ear height, with *H. pomona* having a much larger ear compared to *H. kunzi*: 20.0–21.5 mm (n = 3) versus 15.0–19.5 mm (mean = 17.6 mm — Table 2), respectively. *Hipposideros pomona* and *H. kunzi*, however, are not closely related based on both mitochondrial and nuclear DNA (Murray *et al*., 2012; this study).

Despite being sister taxa (Fig. 2), having similar appearance, and overlapping in echolocation call frequencies (Kingston *et al*., 2000), individuals of *H. kunzi* and *H. cineraceus*-B are easily distinguished using body size (*H. kunzi* being larger;

Table 2) and nose morphology: *H. cineraceus*-B has a small swelling in its internarial septum (Fig. 9).

Reproduction

In both 2003 and 2004 in peninsular Malaysia, palpably pregnant females were captured in February and March, and lactating individuals were captured from April through September. Similarly, Nurul-Ain *et al*. (2017) found females from Krau Wildlife Reserve and Samad Cave (ca. 10 Km from Krau) to be seasonally monestrous, with a peak in pregnancy in March, and lactation in June, although lactating females were captured from April through October.

Distribution, *ecological notes*, *and conservation status*

Currently, *H. kunzi* has only been documented on the Malay Peninsula, between 3°12'N in peninsular Malaysia (Fig. 1, site 12) and the Isthmus of Kra at 10°41'N in Southern Thailand (this study; Douangboubpha *et al*., 2010). Despite extensive sampling, Douangboubpha and colleagues did not capture *H. kunzi* in Central or Northern Thailand, suggesting that the northern limit of this species' range is restricted to the Sundaic biogeographical region, as delimited by the Isthmus of Kra (Douangboubpha *et al*., 2010). While we did not sample bats in the southern tip of peninsular Malaysia, we expect that *H. kunzi* should occur throughout the peninsula where suitable habitat exists. Lim *et al*. (2014) reported a positive correlation between the abundance of *H. kunzi* (as *H. bicolor*-142) and latitude across 15 forest sites in peninsular Malaysia, with few or no captures at sites in the southern third of the Peninsula (which may be attributable to the lack of karst). In Singapore, *H. bicolor* (= *H. kunzi*) is considered locally extinct due to habitat loss (Pottie *et al*., 2005). Douangboubpha *et al*. (2010) included Sumatra in the distribution of *H. atrox* (= *H. kunzi*), but because of the high level of cryptic diversity within this group it is impossible to determine whether individuals from Sumatra are conspecific with *H. kunzi* without genetic data. Based on limited sampling in Borneo (Fig. 1), there is currently no evidence that *H. kunzi* occurs in Borneo.

In peninsular Malaysia, individuals of *H. kunzi* were captured at all sampling sites (Fig. 1) and were relatively common and widespread in karst regions, but were also common in some non-karst areas (e.g., Krau Wildlife Reserve). Colonies ranged in size from a few individuals to several hundred and were found in caves, mines, and rock crevices. Colonies of *H. kunzi* were almost always found in caves housing other bat species; these included *H. cervinus*, *H. larvatus*, *H. armiger*, *Rhinolophus malayanus*, *R. stheno*, *Myotis siligorensis*, *M. ater*, *Miniopterus medius*, and *Taphozous melanopogon.* Based on captures and wing morphology, *H. kunzi* is believed to forage in forested habitats; Douangboupha *et al*. (2010) suggested that *H. kunzi* forages in diverse forest types and may be somewhat tolerant of anthropogenically modified landscapes that retain vegetative structure (e.g., secondary forest, rubber and orchard plantations). Given the species' distribution across the Malay peninsula into Southern Thailand, widespread occurrence and local abundance, we currently recommend *H. kunzi* be evaluated as a species of Least Concern, following IUCN Red List Categories and Criteria v. 3.1 (IUCN, 2012). Loss and disturbance of caves and foraging habitats would support a higher category of risk.

We and others have noted the high levels of cryptic diversity in *Hipposideros* (e.g., Esselstyn *et al*., 2012; Murray *et al*., 2012; Foley *et al*., 2017). We hope that our taxonomic delineation of a new member of the *bicolor* species group, *H. kunzi*, will motivate further efforts to resolve the taxonomy of remaining cryptic lineages. Such efforts are essential to the conservation of the remarkable diversity that exists within this already speciose genus.

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Appendix

Individuals included in the genetic and/or skull morphology analyses are presented with source and locality information (reference to sites in Fig. 1 are given in parentheses when available). Voucher numbers are provided for individuals that were collected: AMNH — American Museum of Natural History, New York, NY, USA, BMNH — Natural History Museum, London, UK, FMNH — Field Museum, Chicago, IL, USA, HZM — Harrison Zoological Museum, Kent, UK, MCZ — Museum of Comparative Zoology, Harvard, MA, USA, MZB — Muzeum Zoologicum Bogoriense, Bogor, Indonesia, RMNH — National Museum of Natural History Naturalis, Leiden, Netherlands, SEN — Senckenberg Museum, Frankfurt, Germany, TK — tissue collection and TTU — specimen numbers; Texas Tech. University, Lubbock, TX, USA, and USNM — Smithsonian Institute, Washington D.C., USA. All specimens from peninsular Malaysia with THK or MBCRU field numbers were collected by A. Zubaid, and the specimens or duplicate wing punches were deposited at UKM (Universiti Kebangsaan Malaysia, Bangi, Selangor, Malaysia). The original taxonomy of type specimens (type) are listed. Haplotypes (Hap) are given for individuals of *H. bicolor* (=*H. bicolor*-131) and *H. kunzi* (=*H. bicolor*-142). GenBank accession numbers are given for one representative of each unique haplotype

Current taxonomy	Museum/Field number	Locality	Skull	Hap	GenBank	Type
H. armiger	THK 8839	Malaysia: Perlis (10)			JN714747	
H. ater	SEN 83700	Malaysia: Sabah (14)			JN714748	
H. ater	FMNH 166410	Philippines: Luzon Is.			JN714750	
H. ater	MZB 26345	Indonesia: E. Kalimantan			JN714749	
H. a. amboiensis	RMNH 33657[a]	Indonesia: Ambon Is.	x			*H. amboiensis*
H. a. amboiensis	RMNH 33658[a]	Indonesia: Ambon Is.	x			*H. amboiensis*
H. bicolor bicolor	RMNH 33654[a]	Indonesia: Java Is.	x			*H. b. bicolor* (lectotype)
H. b. bicolor	RMNH 32164	Indonesia: Java Is.	x			*H. javanicus*
H. b. bicolor	RMNH 32178	Indonesia: Java Is.	x			*H. javanicus* (holotype)
H. b. bicolor	RMNH 32385	Indonesia: Banka Is.	x			
H. b. bicolor	RMNH 32694	Indonesia: Java Is.	x			*H. javanicus*
H. b. bicolor	RMNH 32712	Indonesia: Java Is.	x			*H. javanicus*
H. b. bicolor	RMNH 32713	Indonesia: Java Is.	x			*H. javanicus*
H. b. bicolor	RMNH 32714	Indonesia: Java Is.	x			*H. javanicus*
H. b. bicolor	RMNH 32715	Indonesia: Java Is.	x			*H. javanicus*
H. b. bicolor	RMNH 32716	Indonesia: Java Is.	x			*H. javanicus*
H. b. atrox	BMNH 1.3.9.4	Malaysia: Selangor	x			*H. gentilis atrox*
H. b. erigens	MCZ 35195	Philippines: Mindoro Is.	x			*H. erigens*
H. b. erigens	MCZ 35196	Philippines: Mindoro Is.	x			*H. erigens*
H. b. erigens	MCZ 35197	Philippines: Mindoro Is.	x			*H. erigens* (holotype)
H. b. erigens	MCZ 35198	Philippines: Mindoro Is.	x			*H. erigens*
H. b. major	BMNH 94.1.7.6	Indonesia: Engano Is.	x			*H. g. major*
H. bicolor	FMNH 180193	Philippines: Luzon Is.	x		JN714755	
H. bicolor-131	–	Malaysia: Perak (9)		M5	MH375717	
H. bicolor-131	–	Malaysia: Perak (9)		M6	MH375718	
H. bicolor-131	MBCRU A0844	Malaysia: Pahang (4)	x			
H. bicolor-131	MBCRU A0855	Malaysia: Pahang (4)	x			
H. bicolor-131	MBCRU A4691	Malaysia: Pahang (4)		M3	MH375719	
H. bicolor-131	THK 6638	Malaysia: Pahang (4)	x			
H. bicolor-131	THK 6689	Malaysia: Pahang (4)	x			
H. bicolor-131	THK 6692	Malaysia: Pahang (4)	x			
H. bicolor-131	THK 18809	Malaysia: Pahang (4)	x			
H. bicolor-131	THK 40448	Malaysia: Pahang (4)	x	M1		
H. bicolor-131	THK 40449	Malaysia: Pahang (4)	x	M4		
H. bicolor-131	THK 40657	Malaysia: Pahang (4)	x	M2	MH375720	
H. bicolor-131	THK 40775	Malaysia: Pahang (4)	x	M2		
H. bicolor-131	THK 41017	Malaysia: Pahang (4)	x			
H. bicolor-131	THK 41022	Malaysia: Pahang (4)	x			
H. bicolor-131	THK 41750	Malaysia: Pahang (4)	x			
H. bicolor-131	TK 152015	Malaysia: Pahang (4)		M1		
H. bicolor-131	TK 152016	Malaysia: Pahang (4)		M1	MH375721	
H. bicolor-131	TK 152026/TTU 108186	Malaysia: Pahang (4)	x	M1		
H. bicolor-131	TK 152029/TTU 108189	Malaysia: Pahang (4)	x[b]	M1		
H. bicolor-131	TK 152030	Malaysia: Pahang (4)		M1		
H. bicolor-131	TK 152031/TTU108191	Malaysia: Pahang (4)	x	M4	MH375722	
H. bicolor-131	TK 152032/TTU 108192	Malaysia: Pahang (4)	x	M1		
H. bicolor-131	TK 152036/TTU 108196	Malaysia: Pahang (4)	x[b]	M1		
H. bicolor-131	TK 152039	Malaysia: Pahang (4)		M1		

Appendix. Continued

Current taxonomy	Museum/Field number	Locality	Skull	Hap	GenBank	Type
H. bicolor-131	TK 152041	Malaysia: Pahang (4)		M1		
H. bicolor-131	TK 153506	Malaysia: Pahang (3)		M8	MH375723	
H. bicolor-131	TK 153523	Malaysia: Pahang (3)		M7	MH375724	
H. bicolor-131	SEN 83691	Malaysia: Sabah (14)		B4	MH375725	
H. bicolor-131	BMNH 83.340	Malaysia: Sabah (14)	x[b]			
H. bicolor-131	TK 152119/TTU 108267	Malaysia: Sarawak (16a)	x	B6	MH375726	
H. bicolor-131	TK152141/TTU 108289	Malaysia: Sarawak (16a)	x	B6		
H. bicolor-131	TK 152146/TTU 108294	Malaysia: Sarawak (16a)	x	B6		
H. bicolor-131	TK 152148/TTU 108296	Malaysia: Sarawak (16a)	x	B6		
H. bicolor-131	TK 152149/TTU 108297	Malaysia: Sarawak (16a)	x	B6		
H. bicolor-131	TK 152153	Malaysia: Sarawak (16a)		B6		
H. bicolor-131	TK 152684	Malaysia: Sarawak (16b)		B7	MH375727	
H. bicolor-131	TK 152685	Malaysia: Sarawak (16b)		B6		
H. bicolor-131	–	Indonesia: Kalimantan (17)		B3	MH375728	
H. bicolor-131	–	Indonesia: Kalimantan (17)		B2	MH375729	
H. bicolor-131	MZB 26357	Indonesia: Kalimantan (17)	x			
H. bicolor-131	MZB 26361	Indonesia: Kalimantan (17)	x	B1	MH375730	
H. bicolor-131	MZB 2675	Indonesia: Kalimantan (17)		B1		
H. bicolor-131	USNM 590233	Malaysia: Sarawak (15)	x[b]	B5	MH375731	
H. bicolor-131	USNM 590388	Malaysia: Sarawak (15)		B5		
H. bicolor-131	USNM 590234	Malaysia: Sarawak (15)	x[b]			
H. bicolor-131	USNM 590235	Malaysia: Sarawak (15)	x[b]			
H. bicolor-131	USNM 590236	Malaysia: Sarawak (15)	x[b]			
H. bicolor-131	USNM 590237	Malaysia: Sarawak (15)	x[b]			
H. bicolor-131	USNM 590238	Malaysia: Sarawak (15)	x[b]			
H. bicolor-131	USNM 590239	Malaysia: Sarawak (15)	x[b]			
H. bicolor-131	USNM 590240	Malaysia: Sarawak (15)	x[b]			
H. bicolor-131	USNM 590241	Malaysia: Sarawak (15)	x[b]			
H. bicolor-142	THK 40651	Malaysia: Pahang (1)	x	B		
H. bicolor-142	THK 40652	Malaysia: Pahang (1)	x	B		
H. bicolor-142	THK 40653	Malaysia: Pahang (1)	x	B		
H. bicolor-142	THK 40655	Malaysia: Pahang (1)	x	B		
H. bicolor-142	THK 41339	Malaysia: Pahang (1)	x	B		
H. bicolor-142	THK 41342	Malaysia: Pahang (1)	x			
H. bicolor-142	MBCRU A4345	Malaysia: Pahang (2)		B		
H. bicolor-142	TK 153519	Malaysia: Pahang (3)		A		*H. kunzi*
H. bicolor-142	TK 153504	Malaysia: Pahang (3)		A		
H. bicolor-142	TK 152992	Malaysia: Pahang (3)		A		*H. kunzi*
H. bicolor-142	TK 152065/TTU 108222	Malaysia: Pahang (4)		A	MH375732	*H. kunzi* (holotype)
H. bicolor-142	TK 152001/TTU 108417	Malaysia: Pahang (4)	x	B	MH375733	*H. kunzi*
H. bicolor-142	TK 152051/TTU 108209	Malaysia: Pahang (4)	x	B		*H. kunzi*
H. bicolor-142	MBCRU A4539	Malaysia: Pahang (4)		R	MH375734	
H. bicolor-142	MBCRU A3693	Malaysia: Pahang (4)		P	MH375735	
H. bicolor-142	MBCRU A4536	Malaysia: Pahang (4)		M	MH375736	
H. bicolor-142	MBCRU A4667	Malaysia: Pahang (4)		O	MH375737	
H. bicolor-142	MBCRU A4709	Malaysia: Pahang (4)		N	MH375738	
H. bicolor-142	THK 40672	Malaysia: Pahang (4)	x	B		
H. bicolor-142	THK 41912	Malaysia: Pahang (4)	x			
H. bicolor-142	THK 41915	Malaysia: Pahang (4)	x			
H. bicolor-142	THK 6619	Malaysia: Pahang (4)	x			
H. bicolor-142	THK 41744	Malaysia: Pahang (4)		Q		
H. bicolor-142	THK 40266	Malaysia: Pahang (5)	x	A		
H. bicolor-142	THK 40269	Malaysia: Pahang (5)	x	A		
H. bicolor-142	THK 40270	Malaysia: Pahang (5)	x	A		
H. bicolor-142	THK 40281	Malaysia: Pahang (5)	x	A		
H. bicolor-142	THK 40284	Malaysia: Pahang (5)	x	A		
H. bicolor-142	THK 40285	Malaysia: Pahang (5)		G	MH375739	
H. bicolor-142	THK 40288	Malaysia: Pahang (5)		H	MH375740	
H. bicolor-142	THK 41280	Malaysia: Pahang (5)	x	A		
H. bicolor-142	THK 40459	Malaysia: Kelantan (6)	x			

Appendix. Continued

Current taxonomy	Museum/Field number	Locality	Skull	Hap	GenBank	Type
H. bicolor-142	THK 41307	Malaysia: Kelantan (6)	x	A		
H. bicolor-142	THK 41310	Malaysia: Kelantan (6)	x	A		
H. bicolor-142	THK 41312	Malaysia: Kelantan (6)	x	A		
H. bicolor-142	THK 41316	Malaysia: Kelantan (6)	x	A		
H. bicolor-142	THK 41318	Malaysia: Kelantan (6)	x			
H. bicolor-142	THK 41284	Malaysia: Kelantan (7)	x	E	MH375741	
H. bicolor-142	THK 41285	Malaysia: Kelantan (7)	x	D	MH375742	
H. bicolor-142	THK 41286	Malaysia: Kelantan (7)	x			
H. bicolor-142	THK 41287	Malaysia: Kelantan (7)	x	E		
H. bicolor-142	THK 41290	Malaysia: Kelantan (7)		K	MH375743	
H. bicolor-142	THK 41291	Malaysia: Kelantan (7)	x			
H. bicolor-142	THK 41297	Malaysia: Kelantan (7)	x			
H. bicolor-142	THK 41516	Malaysia: Perak (8)	x			
H. bicolor-142	THK 41520	Malaysia: Perak (8)		L	MH375744	
H. bicolor-142	THK 41532	Malaysia: Perak (8)	x	A		
H. bicolor-142	THK 41536	Malaysia: Perak (8)	x	A		
H. bicolor-142	THK 41537	Malaysia: Perak (8)	x	A		
H. bicolor-142	THK 41538	Malaysia: Perak (8)	x	A		
H. bicolor-142	THK 41540	Malaysia: Perak (8)	x	A		
H. bicolor-142	–	Malaysia: Perak (9)		I	MH375745	
H. bicolor-142	–	Malaysia: Perak (9)		A		
H. bicolor-142	THK 8772	Malaysia: Perlis (10)	x	W	MH375746	
H. bicolor-142	THK 8866	Malaysia: Perlis (10)		X	MH375747	
H. bicolor-142	THK 40816†	Malaysia: Perlis (10)		T	MH375748	
H. bicolor-142	THK 40817	Malaysia: Perlis (10)		Q	MH375749	
H. bicolor-142	THK 40819†	Malaysia: Perlis (10)		S	JN714753	
H. bicolor-142	THK 40933	Malaysia: Perlis (10)		V	MH375750	
H. bicolor-142	THK 40935	Malaysia: Perlis (10)	x			
H. bicolor-142	THK 40936	Malaysia: Perlis (10)	x			
H. bicolor-142	THK 40939	Malaysia: Perlis (10)	x			
H. bicolor-142	THK 40943	Malaysia: Perlis (10)	x			
H. bicolor-142	THK 40945	Malaysia: Perlis (10)	x			
H. bicolor-142	THK 41503	Malaysia: Perlis (10)		U	MH375751	
H. bicolor-142	–	Thailand: Ao Luk (11a)		Y	MH375752	
H. bicolor-142	–	Thailand: Ao Nang (11b)		Z	MH375753	
H. bicolor-142	THK 40407	Malaysia: Selangor (12)	x			
H. bicolor-142	THK 40412	Malaysia: Selangor (12)	x	C	MH375754	
H. bicolor-142	THK 40418	Malaysia: Selangor (12)	x	J	MH375755	
H. bicolor-142	THK 40420	Malaysia: Selangor (12)	x	A		
H. bicolor-142	THK 41548	Malaysia: Selangor (12)	x	C		
H. bicolor-142	THK 41549	Malaysia: Selangor (12)	x	C		
H. bicolor-142	THK 40457	Malaysia: Perak (13)		F	MH375756	
H. cervinus	THK 41734	Malaysia: Pahang (4)			MH375757	
H. cineraceus	–	Indonesia: C. Kalimantan			JN714762	
H. cineraceus	20040259	Indonesia: Sulawesi			JN714765	
H. cineraceus	HZM 3.34873	Myanmar: Mon			JN714764	
H. cineraceus-A	–	Malaysia: Perak (8)			JN714760	
H. cineraceus-A	THK 8854	Malaysia: Perlis (10)	x			
H. cineraceus-A	THK 8855	Malaysia: Perlis (10)	x			
H. cineraceus-A	THK 8856	Malaysia: Perlis (10)	x			
H. cineraceus-A	THK 22855	Malaysia: Perak (8)	x			
H. cineraceus-A	THK 22856	Malaysia: Perak (8)	x			
H. cineraceus-A	THK 22869	Malaysia: Perlis (10)	x			
H. cineraceus-A	THK 22871	Malaysia: Perlis (10)	x			
H. cineraceus-A	THK 22872	Malaysia: Perlis (10)	x			
H. cineraceus-A	THK 22874	Malaysia: Perlis (10)	x			
H. cineraceus-A	THK 22875	Malaysia: Perlis (10)	x			
H. cineraceus-B	THK 41702	Malaysia: Pahang (4)	x		JN714761	
H. halophyllus	BMNH 78.2344	Thailand: Phet buri	x			
H. halophyllus	BMNH 78.2346	Thailand: Ratchaburi	x			

APPENDIX. Continued

Current taxonomy	Museum/Field number	Locality	Skull	Hap	GenBank	Type
H. halophyllus	THK 8771	Malaysia: Perlis (10)	x			
H. halophyllus	THK 8853	Malaysia: Perlis (10)	x			
H. halophyllus	THK 8857	Malaysia: Perlis (10)	x			
H. halophyllus	THK 22851	Malaysia: Perlis (10)	x			
H. halophyllus	THK 22863	Malaysia: Perlis (10)	x			
H. halophyllus	THK 22865	Malaysia: Perlis (10)	x			
H. halophyllus	THK 22866	Malaysia: Perlis (10)	x			
H. halophyllus	THK 22868	Malaysia: Perlis (10)	x			
H. macrobullatus	AMNH 102367	Indonesia: Sulawesi Is.	x			*H. b. macrobullatus*
H. pomona	BMNH 18.8.3.4	S. India: Mysore	x			*H. pomona*
H. p. sinensis	BMNH 92.2.1.3	China: Foochow	x			*H. g. sinensis*
H. p. gentilis	BMNH 93.11.15.2	Myanmar	x			*H. g. gentilis*
H. pomona	–	China: Yunnan Prov.			JN714787	
H. pomona	THK 41952	Malaysia: Perlis (10)	x		JN714791	
H. pomona	USNM 583861	Myanmar: Mon State			JN714790	
H. pomona	BMNH 1987.245	Malaysia: Perlis (10)	x			
H. pomona	BMNH 1987.246	Malaysia: Perlis (10)	x			

[a] — Part of the original *H. bicolor bicolor* lectotype series

[b] — Not included in statistical analyses (Table 3) due to missing data

† — Individuals of *H. bicolor*-142 that had outlier echolocation call frequencies (133.2 kHz)